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THE STUDY OF SEAWEEDS

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AN

INTRODUCTION TO THE STUDY

OF

SEAWEEDS

S 7749

BY

GEORGE MURRAY, F.R.S.E., F.L.S.

KEEPER OF THE DEPARTMENT OF BOTANY, BRITISH MUSEUM

WITH EIGHT COLOURED PLATES AND EIGHTY-EIGHT OTHER ILLUSTRATIONS

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PREFACE

SINCE the last introduction to the study of sea-weeds was written, many years ago, the aspect of the whole subject has been completely changed by the progress of research. I have attempted in the following pages to keep the rule of describing only what I have personally verified by examination or by inspection of the original account, and this has been possible in nearly every case.

It would have been more in accordance with usage to begin with the sub-class *Rhodophyceæ*, but I have permitted considerations of convenience to prevail. The *Rhodophyceæ* present so many difficulties, to be understood only after the study of other groups, that I have chosen *Phæophyceæ*, with its familiar forms of sea-wracks and tangles, for the first sub-class. The *Chlorophyceæ* and *Diatomaceæ* follow naturally. The *Rhodophyceæ* next make a

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series by themselves, and finally come the simple *Cyanophyceæ*.

The account of the *Rhodophyceæ* is based on the scattered papers of Schmitz (p. 37), who by utilising his own researches and the splendid investigations of Thuret and Bornet has almost wholly altered the classification of this sub-class. A mere outline of his results has been published with the effect of destroying the earlier classification and of incompletely establishing his own. The full justification of his system will, however, be published soon, having been left by him almost finished at his lamented early death. I have thought it better to give here from the fragments of his work accessible to me, and from other sources, an account of the sub-class under his system, rather than revert to the old classification.

I have to thank the Council of the Linnean Society, the editors of the *Annals of Botany* and *Journal of Botany*, and Messrs. Dulau and Co., publishers of the *Phycological Memoirs*, for their kindly granted permission to reproduce copies of my own and other figures. I am also indebted to M. Bornet, Prof. Reinke, Graf zu Solms-Laubach, Dr. John Murray, Mr. Edward Trewendt of Breslau, Dr. Hauptfleisch, Dr. Kuckuck, Mr. Richards,

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GEORGE MURRAY.

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SEAWEEDS

INTRODUCTION

THE study of seaweeds is of very modern origin, and nothing beyond casual recognition of their existence is to be found in the literature and memorials of early times. The Greeks have left us engraved figures of Gorgons whose heads were decorated with seaweeds; there is but one mention of them in the Bible, when Jonah exclaims, "The depths closed me round about, the weeds were wrapped about my head"; and the references in Latin literature, even that of the poets, such as the "Alga projecta vilior" of Virgil and the "inutilis Alga" of Horace are merely contemptuous. While other plants received notice and were the subjects of study in these early times and during the middle ages, the flora of the sea remained within its confines—a *hortus inclusus* within a barrier that still jealously hides much from our knowledge. In Sir Hans Sloane's great herbaria of many travellers and collectors, preserved in the

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British Museum, there is the earliest authentic evidence of the collecting of seaweeds, the beginning of the study; and the foundation of its literature was laid by later systematic writers, including Linnæus. It was only to be expected that many marine animals, such as Zoophytes, which resemble seaweeds frequently in outward form, should have been indiscriminately classed with them by these writers, and it was not until the present century, when our knowledge of minute structure had advanced, that a strict division became possible between the stony coralline Algæ and similarly encrusted animals. Gmelin's *Historia Fucorum* (1768) and Esper's *Abbildungen der Tange* (1797) were the first noteworthy efforts to gather within a book devoted to the study of Algæ all that was then known, and as the result of the stimulus so imparted to research, the first years of the present century witnessed greater activity and progress in the accumulation of knowledge of the forms of seaweeds and their classification. Lamouroux published his *Dissertations sur plusieurs espèces de Fucus* in the year "XIII"(= 1805) of the new era of the French Revolution, and a few years later there was begun the best of all the early books, Dawson Turner's *Fuci* (1808–1819), which not only cleared up many of the difficulties of preceding writers, but presented a large body of new facts acquired from the study of specimens brought home by Robert Brown and other great botanists and travellers of that time. Perhaps the last of those who may be called the pioneers of Phycology was Lyngbye, whose *Tentamen*

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Hydrophytologiæ Danicæ was published in 1819 and dedicated to "Frederic VI., King of Denmark, and of the Goths and Vandals." Just as Linnæus was the last of the older naturalists as well as the first of the new, so the elder Agardh makes a link for us in the history of Phycology. With his greater son, happily still alive, he laid the foundations of the present system of classifying seaweeds, while their fellow-countryman Fries was performing a like service for the study of Fungi, continuing the work of Linnæus in the spirit of Linnæus and in the land of the great naturalist. Germany contributed Kützing to the group of great systematic writers of the same period, and though his work is characterised more by his extraordinary industry than by any new departure of system or method, it has greatly influenced the study by increasing the sum of knowledge and the facilities of reference. Our countrymen Harvey and Greville achieved yet greater advances. The former, by his travels and his genius as a collector, describer, and depictor of marine Algæ, surpassed all others in this field; while the latter, in addition to his great services to other departments of cryptogamic botany, has left observations of the minute structure of seaweeds that no subsequent research has shaken, and has done much towards establishing a natural system of classification. Thuret, and his fellow-worker Bornet, brought to its present state of development the methods of minute study of structure and development that only need wider application in the future to ensure the advancement of Phycology.

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The first observation commonly made by a student of seaweeds is of the variation of their colours. The green hue that prevails throughout land vegetation, except in the colours of flowers and the bark of trees, is varied in the case of seaweeds with olive-brown, and red forms. An artificial classification of them according to their colours leads to the striking result that it nearly coincides with the natural classification of them according to their structure and development. Such an artificial classification became firmly established, and has left its mark on the names of the natural primary divisions or sub-classes of Algæ, viz. the *Rhodophyceæ* or Red Seaweeds; the *Phæophyceæ*, or olive-brown; the *Chlorophyceæ* or green; and the *Cyanophyceæ* or blue-green. A simple experiment proves that fundamentally they are all green, and that the red colouring matter *phycoerythrine*, the brown *phycophæine*, the yellowish-brown *phycoxanthine*, and the blue *phycocyanine* are each something added to the chlorophyll or leaf-green that characterises vegetation in general, and by virtue of which plants form the organic substances necessary for their nutrition. These additional colouring matters can be extracted by fresh water, leaving the previously red, olive, &c. plants green, and they differ from the green colour in this respect, since it is insoluble in water. Though there occur exceptionally a few red forms, numerous blue-green, and (in the diatoms only) many brown forms in fresh-waters, there still remains the broad fact that these colouring matters are characteristic of seaweeds, and it is in the conditions of plant-life in the waters of

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the sea that an explanation of their nature must be sought. It has been found that the colours of seaweeds are more or less indicative of their range in depth in the sea, and, allowing for numerous exceptions, that there is a zonal distribution of Algæ according to their colours. The uniformity of this distribution is disturbed by the fact that the conditions are not equal for all in the face of the deter mining influence, as will presently be made plain As a general rule the inshore seaweeds near high-water mark are green in colour like land vegetation and lower down between tide-marks there is a belt of olive forms sheltering red plants beneath them. Where rocks overhang the bottom, and in small pools these red forms also occur at this level. At extreme low-water mark, and beyond it, are found the brown tangles sheltering red forms again, while at the lowest depths of plant-life in the sea the red forms occur without shelter. Between 20 to 50 fathoms seaweeds become more and more rare, while below that depth their occurrence is exceptional. That the main influence determining this regulation of pigment is the nature of the supply of sunlight, necessary to the action of chlorophyll in the work of nutrition, is apparent from the following facts. The interception of sunlight by sea-water brings about a state of total darkness at 700 fathoms, probably less, and though seaweeds do not penetrate to a depth approaching this limit of light, a further consideration will account for their failure. Not only is the quantity of sunlight reduced by its passage through the water, but its quality is affected, as spectroscopic investigation

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has shown. It is precisely those rays that are most efficient in the work of assimilation by plants that are first intercepted, and only the blue and green rays travel to greater depths. It may be taken, then, that the red, brown, and yellow colouring matters, added to the fundamental green, are adaptations to the supply of sunlight. Whether they act in the direction of heightening the susceptibility of chlorophyll to a diminished supply of the useful rays, or as a protection against a relative excess of the blue rays, has not been settled experimentally, but the balance of probability is in favour of the latter theory, since it has been discovered that certain pigments in other plants act as a shield against illumination of this character. A microscopic green Alga, *Halosphæra viridis*, has been obtained from the great depths beyond the reach of sunlight, and the speculation has been hazarded that the luminosity of animals inhabiting those regions might in its case be an efficient substitute for sunlight, but the idea is wholly unsupported by experimental evidence. The explanation that the plants in question were swept there by currents of submerged waters is much more in accordance with oceanographical facts. The fact that colour, which affords a character of notorious instability in determining claims merely to specific rank among land plants, should be found associated in the Algæ with characters of more than ordinal importance (though not constituting such characters by itself) is not so puzzling when it is remembered that it plays here a *rôle* of vital importance in the matter of nutrition.

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As light is the factor that determines the zonal distribution of seaweeds, and thus influences their local habitats, so temperature is the leading influence, among others of minor potency, that affects their geographical distribution. They inhabit a medium of stable temperature, in which they are not called upon to adjust themselves to any great periodical or fortuitous changes, varying little from day to night and from season to season. On this ground alone they might be presumed to be peculiarly sensitive to change of temperature, and experiments in the culture of seaweeds in aquaria show that a nice regulation of temperature is necessary to success. Comparisons of the marine flora of areas of different temperature confirm this view though they do not exclude other possibilities, since the general character of such floras is modified by other influences—the nature of the bottom to some extent, the degree of salinity of the water, the presence, absence and amount of the tides, &c. Marine vegetation, like fresh-water vegetation, is removed from the influence of relative humidity which determines frequently the character of a land flora, but on the other hand it is subject to control by factors such as relative salinity and the like. The contour of the earth's surface, which brings about the existence of alpine floras for example, and frequently affords many climates at the same latitude on land, has no corresponding influence on the marine flora, since conditions of illumination check range in depth. On the whole, temperature may be said to be left more to itself as a determining influence of the character of marine

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floras than of land floras, and when its operation is tested by a survey of the pelagic vegetation, this view is much enforced by the result. Pelagic free floating Algæ removed from the influence of coast and river waters, rise and fall of tides, nature of bottom, &c., and left to the nearly exclusive operation of temperature in stamping their character, are found to respond to this influence and to vary with areas of temperature in the sea. As an extreme term in resistance to adverse conditions of temperature and supply of light, it is interesting to note Kjellman's observation of the normal growth and fructification of Algæ during the dark arctic night and at a mean temperature of $-1°C$. Observations of any notably high temperatures resisted in the sea are of course of small physiological interest compared with the temperatures resisted by fresh-water Algæ inhabiting hot springs.

In the culture of seaweeds in aquaria it has been found that forms from deep water are peculiarly susceptible to rise of temperature and undue illumination, so much so that merely for their transport it is necessary to choose a cloudy day, especially if in summer, and the use of ice is almost always advisable. A cool chamber from which direct sunlight is excluded is a condition of success in the culture of most seaweeds. One way in which these plants may be killed by too much care is in the attention paid to aeration of the water. Very little is necessary, since the air so introduced has been found to carry off too much CO_2. A sudden change of water is also mischievous; and added water (whether fresh-water to

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make up for evaporation, or salt-water) should be supplied drop by drop. One of the best ways of cultivating seaweeds is by suspending them in baskets in the sea at proper depths from anchored buoys. (*See* Reinke, in *Botan. Centralblatt*, 1890 ; and Oltmanns, in *Pringsheim's Jahrbücher*, xxiii. 1891.)

It has been commonly supposed that the composition of sea-water, and particularly its degree of concentration, has a powerful influence on the distribution of seaweeds. The North Sea, where the salinity reaches 3·5 per cent., is, for example, much richer in its marine flora than the Baltic—even the western part, where the salinity is 1·7 per cent., and still more the eastern and northern parts, where the salinity declines to 0·15 per cent. Oltmanns[1] has shown, however, that the degree of salinity has much less influence than has been believed, but that rapid variations of this condition are hostile to the existence of seaweeds. Where fresh water runs into the sea, it arrives in conditions varying with its abundance, with the currents it meets and forms, and with the direction of winds. There are thus set up differences in the density of the water, and these differences, acting on the cells of seaweeds, are of very detrimental effect. Oltmanns' observations at Warnemunde, near Rostock, are of great interest in this respect. A canal there connects the sea with a lake that receives almost all the fresh-water of Mecklenburg, and many species of seaweeds grow in this lake at places where the salinity is almost nil, while almost all are absent from the canal,

[1] *Sitzungsber. d. K. preuss. Akad. d. Wiss.* (Berlin. 1891.)

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which conveys sometimes salt-water and sometimes fresh.

The ocean currents are of primary importance as agents of distribution, not only as streams of stable temperature, but as vehicles of transport. Currents of air and of water are justly regarded as potent means of dispersal of land plants, and their efficacy in this respect is the result of special adaptation on the part of the plant, such as winged seeds, &c. No such adaptations are called for in the case of Algæ towards ocean currents, though the air-floats of *Fucaceæ* and *Laminariaceæ*, which secure a buoyancy in the first place for vegetative purposes, probably serve in certain cases the end of distribution as well, particularly in the gulf-weeds. As examples of the influence of currents there may be cited the differences in the marine flora between the east and west coasts of South Africa—the west under the influence of a cold stream from the south, and the east affected by the warm Mozambique current from the north; again, the marine flora of Bermuda in the track of the Gulf Stream—the most northern coral island in the world—is much more markedly West Indian than the North American coast flora under the same parallel, outside the influence of this current; and, to trace the Gulf Stream further on its path, there may be noted the contrast between the characteristically temperate marine flora of the Shetland Islands and the Arctic flora of Cape Farewell in the same parallel, but subject to the cold East Greenland current. If the matter were less obvious the proof of it could be reinforced with numerous other instances.

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The inquiry is worth prosecuting whether man affects the distribution of seaweeds. Iron vessels are much less adequately protected against fouling by the growth of seaweeds than wooden ships, which secure a considerable degree of immunity by the exfoliation of their copper sheathing, and in spite of many ingenious devices, the iron ship and steamer require frequent docking, and when sluggish, a greatly increased expenditure of coal for driving. Though cosmopolitan species like the forms of *Enteromorpha* (the "grass" of seafaring language) abound near the water-line, many others, often seaweeds of large size, occur beneath, especially when the vessel has been long at moorings. With such vessels traversing the sea in all directions, it is more than probable that the acclimatisation of aliens occurs, especially when the passage is from and to similar regions. Vessels making the passage from the Cape of Good Hope to this country across the tropics arrive with cosmopolitan forms merely, as might have been expected; but the Atlantic passage between this country and North America, for example, deserves watching, and still more the Suez Canal passage.

In this way man may aid the ocean currents in bridging the depths of the sea, which offer a barrier to the distribution of coast Algæ. Coast deserts of sand, mud, and very friable rock in the sea are barriers frequently of great extent. There are such for example in the Gulf of Mexico from Florida to Yucatan, in the Siberian Sea, and along the muddy coast of western tropical Africa. Great irruptions of fresh-

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water from large rivers also mark dividing lines of coast areas of distribution, and profoundly modify the character of the flora in their vicinity. The ocean forms a far less effectual barrier, however, to the dispersal of land plants than continental areas do to seaweeds, which have no means of bridging them, though many species are of sufficient range to enable them to double capes from one region to another geographically remote. The continental barrier of Africa interposed between the tropical Atlantic and the Indian Ocean offers a passage round the Cape of Good Hope, warm enough to sustain a marine flora with many subtropical types, but subject to the distracting influence of opposite hot and cold currents. The result of a comparison of the floras of these two tropical regions discloses the fact, that while the genera are largely in common, the species are in a high proportion different, and this is naturally most strikingly true of orders like the *Siphoneæ*, which are only sparingly represented outside the tropics. Areas of different temperature in the ocean have thus to be added to continental areas as natural barriers, since the ocean is never wholly fenced about with land. Such areas of different temperature, however, are effective barriers of themselves, as a comparison of the north temperate marine flora with the south temperate one shows. The heat barrier of the tropical seas would be less effective if the cold depths of the ocean were available for passage, but such depths are dark, and moreover the colder waters rise to the surface of warm seas, and thus disable the transporting action of cold currents.

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That there is great diversity in the marine coast floras of different regions is well known, and a comparison of three remote and dissimilar regions furnishes an extreme case. It would be difficult to select three instances of less geographical relationship than the Arctic Sea, the West Indies, and Australia. The first has 259 species in 111 genera, the second 788 species in 150 genera, and the third has 1,132 species in 255 genera. The Arctic Sea has 42 genera and 30 species in common with the West Indies, the same number of genera and 21 species in common with Australia, while out of the two larger totals from the West Indies and Australia there are 109 genera and 135 species in common. If we take the forms common to all three there are 32 generic types, but only 12 species out of these large totals sufficiently cosmopolitan to occur so widely. An analysis of the totals shows that in the Arctic regions the genus averages slightly more than 2 species only, while in the West Indies it is rather more than 5, and on Australian coasts rather less. The north temperate Atlantic yields an average of about 4½ species to the genus, while the South African coast gives us only 3, a result which may be attributed to its small coast-line. There is still a great lack of material on which to found such comparisons with many regions of the ocean, and in the absence of full records the making of contrasts is only misleading. Enough has been said to show the diversity of such floras, the means of distribution, and the principal natural barriers that delimit the boundaries of areas.

A comparison of the Arctic and the Antarctic

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marine floras brings out the interesting result that there is a much higher proportion of forms in common between the two areas than might have been expected. This is especially the case with the pelagic or free-floating plant organisms of the open sea, and without citing figures, since exact data are not available, this may be taken to be generally true. Such forms are much less variable than littoral seaweeds. If we compare the two littoral floras they will be found to be of similar extent, viz. 259 species in the Arctic and 269 in the Antarctic. The Arctic species are, as has been said, in 111 genera, an average of $2\frac{1}{3}$ species to the genus. The Antarctic species are in 98 genera, very nearly an average of $2\frac{3}{4}$ species to the genus. The genera common to both are 56, and the species 41. However, pushing the inquiry a little farther, it will be found that while some Arctic forms occur in the South Temperate zone and not in the Antarctic, similarly some Antarctic forms are found in the North Temperate zone and not in the Arctic. Adding these, we get 92 species in common to Arctic and Antarctic, including adjoining regions, and it would be much greater if we included the two Temperate zones fully; but the object is to compare the two cold-water floras as strictly as possible. Of these 92 species, 38 occur in the intervening tropical belt, and if they are subtracted, we get 54 species in common to the two polar and adjoining waters which have not been found within the tropics. If we were to take the great seaweeds *Fucaceæ* and *Laminariaceæ*, the sea-wracks and tangles, we should not find even a single genus in common; the common forms are

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all, or nearly all, smaller seaweeds. The fact, however, is sufficiently striking, that there are 54 species occurring in the two polar areas, which have been separated by a heat-belt so long as there has been climate of any sort on the globe, and if we add the even more striking resemblance of the pelagic forms, the agreement needs some theory to account for it. Marine zoologists have a similar difficulty to face. Blandet, and again recently Dr. John Murray, have brought forward the following interesting theory. In Carboniferous times, they hold, that "the surface temperature of the sea could not well have been less than about 70° F., and the same temperature and the same marine fauna prevailed from equator to poles, the temperature not being higher at the equator. . . . In early Mesozoic times cooling at the poles and differentiation into zones of climate appear to have commenced, and temperature conditions did not afterwards admit of coral reefs in the polar area, but the colder, and hence denser, water that in consequence descended to the great depths of the ocean carried with it a large supply of oxygen, and life in the deep sea became possible for the first time. There have been many speculations as to how a nearly uniform temperature could have been brought about in sea-water over the whole surface of the earth in early geological ages, as well as to how sufficient light could have been present at the poles to permit of the luxuriant vegetation that once flourished in these regions. The explanation that appears to me the most satisfactory is the one which attributes these conditions to the very much greater

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size of the sun in the early stages of the earth's history—an idea first introduced into geological speculations by Blandet (*Bull. Soc. Géol. de France*, sér. 2 t. 25, p. 777, 1867–68), who likewise discussed the relations of Arctic and Antarctic faunas—together with the greater amount of aqueous vapour in the atmosphere and the greater mass of the atmosphere." (Murray, in *Summary of Results, "Challenger" Reports*, 1895.)

Another interesting point in the distribution of seaweeds bearing on this subject is that those having an incrustation of carbonate of lime occur much more plentifully in the warmer oceans—a fact equally true of the marine animals, though the process of deposition is different. This very slight development of carbonate of lime structures in the cold waters of the polar regions is instructive when compared with the massive coral reefs constructed in the polar regions in Palæozoic and later geological times.

It is a commonplace of biological knowledge that the nutrition of the animal kingdom is dependent upon the action of green vegetation in performing the primary office of converting the inorganic into the organic, and thus producing fitting substances for food. A casual observation of the great mass of terrestrial vegetation, and a comparison of it bulk for bulk with the animal life of the land, enables us to recognise the adequacy of the one as a balance to the other. On turning to the conditions that prevail in the ocean, it is at once apparent that a mere fringe of coast vegetation, extending to no great depth, can-

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not suffice as a basis for the nutrition of the enormous mass of marine animal life which not only ranges over the great surface but penetrates into the depths of the ocean far beyond the reach of sunlight. The balance is redressed by the inconceivably great bulk of the pelagic flora, a department of the study of Algæ which has been so much neglected that there is little beyond an outline knowledge of its extent. Inhabiting the surface layers of the ocean from the polar regions to the tropics there is an extensive floating marine vegetation, consisting of individuals each of microscopic dimensions, and only under special circumstances conspicuous in the mass. In the colder seas of the north and south the mass of this flora is composed of *Diatomaceæ* (Figs. 60), which occur in such numbers as to yield on tow-netting a palpable scum, becoming felt-like in consistency on drying. This living diatomaceous scum inhabits the upper layers of the waters, and rains down its dead in the form of siliceous shells on the bottom, forming extensive deposits known as diatomaceous ooze. Such deposits of marine and fresh water diatoms not only occur now on the floor of the ocean, but are preserved in rocks from the Cretaceous period, and are found, in great extent, in deposits of Tertiary and Quaternary age. While such *Diatomaceæ* occur in greatest abundance in these regions, they have besides a wide range over the ocean surface, becoming mixed in temperate seas with *Peridinieæ* (Fig. 56), which also are found in vast shoals. The *Peridinieæ* are a group of organisms that require for their elucidation much more study than has been given to

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them, but there appears to be little doubt of their plant nature. Mixed with these also in temperate seas are the *Coccospheres* (Fig. 58*b*), and inhabiting the warmer seas of the tropics the *Rhabdospheres* (Fig. 58*a*), organisms of highly probable plant nature, but less studied even than the *Peridiniœ*. Their broken-down parts—known to geologists as *Coccoliths* and *Rhabdoliths*—are, like the remains of *Diatomaceœ*, known from the chalk, and now play an important part in laying down the deep-sea deposits of non-polar seas, associated in this (as also in life) with the animal *Foraminifera* of the globigerina oozes. Mingled with these organisms there is a profusion of pelagic *Protophyta*, which sometimes, as in the case of *Trichodesmium erythræum*, form great banks discolouring the ocean over large areas, and in their origin resembling the fresh-water phenomena known as the "breaking of the meres" in Shropshire, and described by de Candolle and others as occurring in the Lake of Morat and other places, by which large sheets of water are tinged green or reddish owing to the colossal multiplication of minute fresh-water Algæ. Such occurrences have been often noted in the ocean, and, though ordinarily inconspicuous, the Algæ that cause them, and other allied forms, are always present in considerable numbers, as disclosed by the use of the tow-net. Other organisms of abundant occurrence in blue water are *Pyrocystis noctiluca* (Fig. 57), a source of the brilliant luminosity of tropical seas; *Halosphæra viridis* (Fig. 55), of a wider range in warm and temperate seas; and other *Protococcaceœ*. The investigation of this pelagic flora

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is in its infancy, and many other types no doubt await discovery. A recent estimate of the bulk of this flora compares the inconspicuous marine organisms of the Sargasso Sea with the bulk of the floating banks of gulf-weed that give this great tract of ocean its name, with the result that the microscopic forms enormously exceed the gulf-weed in aggregate mass. The result is all the more striking since it is known that the Sargasso Sea is poor in these minute forms compared with many other regions of the ocean. As regards the *Sargassa* floating free in this region and elsewhere, the view generally adopted accounts for their presence by the supposition that they have been torn from their natural moorings and drifted by currents, and that they slowly perish in the Sargasso Sea, to be renewed by fresh supplies from the same source. The theory has much to recommend it on purely oceanographical grounds, but the difficulty remains that *Sargassum bacciferum*, which composes the mass of free-floating *Sargassa* in the tropical Atlantic, has never been recorded as growing attached, in a quantity sufficient to account for the supply. Moreover, other *Sargassa* do grow attached in enormous quantities, but they are of only casual occurrence in a free state. There is still the refuge that *S. bacciferum* is a mere "growth-form" modified by passage down currents. This, however, has no farther observation to support it, and, moreover, an examination of *Sargassa* from the centre of this still region of the ocean shows no symptom of recovery of broader fronds after removal from the influence of the currents that bound it.

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Though the pelagic flora is most imperfectly known as regards its constituent elements, it is manifest that its extent is enormously in excess of the coast marine flora so much more highly diversified in its forms, and that it consequently plays a *rôle* of primary importance in the economy of marine life and one of great geological interest.

The distribution of Algæ in time, as made known to us by their fossil remains, is a branch of study which is somewhat starved by the lack of material. A considerable number of so-called fossil Algæ have been described by Brongniart, Saporta, and other palæophytologists, under such names as *Fucites, Chondrites, Confervites, Caulerpites*, &c., with no better evidence of their algal nature than what may be suggested by the outlines of markings. On the other hand, Nathorst has obtained very general support for his denial of the algal nature of such markings, which he ascribes to trails of animals and other casual impressions in many cases. After weeding out these forms, and trusting only to such cases as exhibit microscopic structure, or characteristic casts in the round supported by evidence derived from geology as to the nature of the bed, or at the least very unequivocal impressions in beds of undoubted marine origin, there is very little left to be chronicled in the testimony of the rocks. The first appearance of Algæ is in the Devonian, from which Mr. Carruthers has described *Nematophycus*, an Alga of siphoneous structure; and Sir Joseph Hooker *Pachytheca*, of more doubtful affinity as yet. With the exception of a fossil *Caulerpa* from the Kimme-

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ridge Clay, and some doubtful *Dasycladaceæ* from other beds, there is no valid evidence of other forms until the chalk is reached, with its *Diatomaceæ* and *Lithothamnion* in the Senonian (Cretaceous) beds, *Coccoliths*, and *Rhabdoliths*. There come next the extensive Tertiary deposits of diatoms, and the beautiful verticillate *Siphoneæ* of the same age described by Munier Chalmas; the coralline *Lithothamnion* and the fresh-water *Characeæ*. The later beds furnish little of interest except Quaternary diatomaceous remains. There is room for disappointment in the failure to find indubitable records in earlier rocks of plants of such primitive type as the Algæ, and it is startling to find such forms as the diatoms suddenly burst upon geological history in a profusion of genera and species, many of which survive in their specific forms from their first appearance to this day. From all that is known of the Silurian rocks, for example, the discovery of diatoms in them would appear to be highly probable, but research has failed to discover them. However intractable and therefore suited to preservation their siliceous shells may be, the existence of conditions under which this substance would become fugitive is probable, and the gap, though significant enough, is not more so than the absence of *Muscineæ*, for example, from the coal measures. It but emphasizes the imperfection of the geological record of plant history, and points to caution in generalising from an insufficient array of facts, more than it indicates argument in favour of any particular sequence of primitive plant forms.

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The conditions of environment of seaweeds are, as has been described, by no means so complex as those of land plants, and their general adaptation to their surroundings is expressed in a corresponding simplicity of structure. The aquatic habit, fresh-water and marine, is accompanied in flowering plants by a degradation of structure in their vegetative organs, since the buoyancy of water, aided by the air-spaces of the plants, dispenses with the need of the mechanical aid of vascular tissue, and partly of its conducting function. This tissue is accordingly much reduced in aquatic flowering plants, and there is a corresponding reduction in the epidermal system, since there is no need of a special cuticular or corky layer to protect the plant from undue evaporation. A favourite view of the evolution of plant forms represents their ascent as a process of gradual emancipation from an aquatic habit; and the adoption of this habit by members of highly developed groups as of the nature of a relapse or approximation to their primitive state. The student of seaweeds is not concerned with the point farther than it is founded on the fact that environment has made no demand on these organisms of a kind that calls for much specialisation of their tissues to enable them to adapt themselves to it, and throughout the group there is a simplicity of structure and a plasticity of form of express character. In the most highly organised seaweeds the vegetative tissues may be classified into a cortical assimilative layer and a central conducting

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strand, the mostly highly developed element of the latter being the sieve-tubes found in *Macrocystis* (*Laminariaceæ*). The sculpturing of outward form reaches its highest point in the differentiation (1) of a root-like holdfast, which, however, is not an organ of absorption unless possibly in the case of certain partially parasitic forms (*cf. Notheia, Choreocolax*, Figs. 5*d*, 64); (2) of a stem and (3) of leaf-like appendages. From this type there are varying intermediate forms down to the wholly undifferentiated type, which occurs among both multicellular and unicellular forms. These intermediate forms may be placed into two categories—those exhibiting a root-like differentiation from an otherwise unspecialised body, and those in which there is merely a distinction between base and apex. In some of the lower multicellular Algæ all the cells are alike, and equally capable of vegetative and reproductive functions. Among the unicellular forms there are those which exist free singly, and others united into a kind of spurious tissue or colony by a common investing mucilaginous cell-wall, and occurring either in rows or filaments, or in more or less indefinite masses. The highest development attained by the unicellular forms, if they may be so termed in this connection, is to be found in the multinucleate group of *Siphoneæ*, which includes many forms with differentiated root-like appendages and leaf-like shoots, and others in which the specialisation is carried so far as to represent leaf-like, stem-like, and root-like organs.

Growth in length is either (1) apical, and effected

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by a single apical cell, or a marginal series, or a meristematic group in the multicellular forms, or by the apical protoplasmic contents in siphoneous plants; or (2) intercalary, at a definite growing-point in the frond, as in *Laminariaceæ*, &c., or in a terminal hair or tuft of hairs with a basal growing-point. Sometimes all the cells of the body remain meristematic and engaged in growth. Secondary growth in thickness may take place, as in the stalk of *Laminaria*, by the peripheral cells beneath the rind being capable of division, and thus adding to the internal tissues, as well as forming towards the outside a bark-like rind; or by an adventitious process, as in *Desmarestia*, where the branching filaments grow together into a kind of pseudoparenchymatous tissue, and invest the original cellular axis.

The cohesion of the body is effected in various ways; either by the union of the cells into a parenchymatous tissue, or by the intertwining of filaments, aided in some cases by the development of sucker-like holdfasts called tenacula or haptera (*Udotea*, *Struvea*, &c.), or by incrustations of carbonate of lime (*Corallineæ*, *Squamariceæ*, and *Siphoneæ*). Stability is obtained in *Caulerpa* by the formation of numerous trabeculæ or branching cellulose cross-beams, braces, or struts, traversing the interior of the cell-cavity from one part of the wall to another, and enabling this remarkable Alga to assume a differentiation into leaf-like, stem-like and root-like parts, though it consists of but one great cell-cavity. Intercellular spaces are most prominently

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represented by the air-bladders which secure buoyancy for the *Fucaceæ* and *Laminariaceæ*, while the whole interior of many other forms is hollow. The mucilaginous character of the cortical tissue of many Algæ protects the internal cells from drying while exposed between tides. In the rind of the *Laminariaceæ* there are special gum-passages, while in *Splachnidium* and other forms the whole of the interior is filled with a mucilaginous substance. Adhesion to the substratum is effected by sucker-like haptera, by basal layers of cells, or by rhizoid filaments which penetrate the substratum.

A comparative review of the reproductive processes of seaweeds would be unprofitable by itself, since such a treatment would lack symmetry without reckoning in the fresh-water forms. It would be, moreover, appropriate only in a treatise on the general morphology of all Algæ. Details of such processes are given in the accounts of the different groups, but it is of interest to note now the occurrence in seaweeds of isogamous and oogamous forms of reproduction, and the propagation by spores and other bodies of purely vegetative character. Though these modes of reproduction are represented in their typical forms among seaweeds, certain subordinate types are confined to the fresh-water Algæ. Conjugation by non-ciliated gametes, for example, occurs in the sea only among the *Diatomaceæ*, since the *Conjugatæ*, of which it is characteristic, are all fresh-water Algæ. There appears to be an almost equal amount of diversity of type of reproduction among fresh-water and marine

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forms—if anything, fresh-waters are richer in such types, while on the other hand the sea is incomparably more favourable to diversity of vegetative development and to luxuriance of habit as well.

It was at one time supposed that among the red and green Algæ there were forms in which the chlorophyll was diffused throughout the protoplasmic cell-contents, but research has shown that in all cases examined in these groups and in the *Phæophyceæ* as well, true chromatophores occur, while they are absent, so far as is known, from the *Cyanophyceæ*. These chromatophores (chlorophores, erythrophores, phæophores or melanophores, as the case may be) sometimes contain pyrenoids—minute bodies (appearing within them much as a nucleolus appears within a nucleus) confined to the chromatophores of Algæ with the single known exception of *Anthoceros* (Hepaticæ). The chromatophores occur either singly in each cell or in numbers, and are of definite and characteristic shapes. These shapes are not only of constant character, but the same constancy extends to the fact of their single or numerous occurrence in each cell. The presence or absence of pyrenoids, which may vary in size from time to time, affords a more capricious character, since forms possessing them are found among the *Phæophyceæ*, *Rhodophyceæ*, and *Chlorophyceæ*. Various attempts have been made to attach special significance to the occurrence of pyrenoids, but so far there has not been much success in elucidating this point. There is, for example, no clear ground for the view that their presence is connected with

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an incomplete differentiation of reproductive and vegetative cells in the plants which possess them. It may be so, but the point is by no means established. The special amyloplastic function of the chromatophore, as distinguished from its assimilative one, appears to be limited to that portion immediately investing the pyrenoid. If the change of size of the pyrenoids be associated with the nutritive state of the cell, as appears probable, it would confirm the opinion that they are reserves of proteid.

In collecting seaweeds between tide-marks the nature of the appropriate equipment is so obvious as to need little direction. The most convenient receptacle for specimens is the ordinary waterproof sponge-bag, though a tinned iron milk-can with a good lid has its advantages. In no case should glass bottles be carried in the hand or pocket, since they are a source of danger, and unnecessary. For similar reasons a knife is an undesirable companion in slippery places, and it is not needed if the collector carry a stout stick of the alpenstock pattern, with a chisel screwed into one end for scraping off specimens, and a small landing-net ring provided with a cotton bag instead of a net attached to the other end. The stick is useful for support, and the bag for securing floating specimens that have been detached by the chisel. Wading boots are of great advantage, except where there are deep pools, when the risk attending immersion is greatly increased by their use.

Though a storm is often more productive than a dredging expedition, the specimens are frequently

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much lacerated, and should be collected at once to be of any value, since exposure quickly spoils them. The ordinary form of dredge used in securing zoological specimens serves for seaweeds, but is liable to become choked. Reinke's dredge, armed with cutting teeth like spear-heads surrounding the mouth, has been found to be serviceable, and a simple contrivance shaped like the letter A, with strong fishhooks of the largest size on strong cords attached to the cross-bar, and the ends of the legs weighted, has been recommended, but requires skill and judgment in its use. It is likely to disappoint the experimenter unless under very favourable conditions. A light dredge can be easily worked from a rowing-boat, which is also sufficient for tow-netting with fine silk nets for the capture of the free-floating minute Algæ. The traveller who wishes to examine the minute pelagic Algæ from the surface layers of the ocean can do so by obtaining permission to tap an inlet pipe of a steamship, and allowing the water to run through a fine silk bag for a time, when he will be rewarded with results similar to those from tow-netting. This method has been successfully practised by its inventor, Dr. John Murray, of the *Challenger* expedition.



Fig. 1.—Reinke's Dredge.

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In drying specimens the material should be floated out, and a mount-paper of suitable size placed under it and slowly lifted out by one corner. By means of a camel-hair brush the branches may be kept apart, since they are apt to become entangled at the critical moment of leaving the water. When this happens at one or two spots merely, a drop of water placed on the part will permit of rearrangement without plunging the whole in again. A number of specimens may be dried simultaneously by using, instead of a basin, a shallow zinc tray with a perforated or wire-woven plate large enough for several specimens. It requires practice in lifting it out, and though specimens good enough for botanical purposes may be so obtained, they are never so beautifully arranged as when taken out singly on their mounts. The wet specimens on their mounts should be placed at once between sheets of drying-paper (blotting-paper is too absorbent) with a layer of muslin over each sheet of specimens to prevent their adhering to the upper sheet of drying-paper. As a rule seaweeds need less pressure than flowering plants, and the collector will very soon learn to adjust it. Plenty of drying-paper should be used, and frequently changed—twice during the first twenty-four hours, and once afterwards until the specimens are quite dry.

Though dried specimens can be easily soaked out again for microscopic examination, they are never so good for this purpose as those that have been preserved in fluid. A good method of soaking is to place the part to be examined, over-night or longer, in absolute

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alcohol, to remove as much air as possible. It should then be transferred to salt and water, and permitted to remain in it. A drop or two of glycerine should be added, and the process may be hastened by gently heating, not boiling. The most successful specimens are those that have been kept at about 90° F. for several hours. Material so treated may then be preserved in spirit (at first weak, and gradually strengthened).

Living specimens to be preserved in spirit should be first treated with picric acid. A saturated solution of picric acid in sea-water should be made and subsequently diluted with three or four times its volume of sea-water. The specimens should be immersed in it from a quarter of an hour to two hours, according to size and density; then washed in sea-water and placed first into weak spirit, and by degrees into stronger spirit. Specimens vary greatly as to the result of treatment by picric acid. To obtain thorough fixation of the contents of such Algæ as *Valonia* (Fig. 46) it is necessary to immerse them for several hours in the saturated solution itself.

For mounting microscope slides of seaweeds the best medium is clear glycerine jelly, which has the advantage of being easily manipulated. The examination of Algæ encrusted with carbonate of lime, such as the stony corallines, is facilitated by the use of Perenyi's decalcifying fluid (4 vols. 10 per cent. nitric acid, 3 vols. absolute alcohol, and 3 vols. 5 per cent. chromic acid), which gives better results than weak hydrochloric acid or any other method in common use. It is particularly valuable in examining Algæ

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like *Gomontia* (Fig. 50), which bore into and inhabit shells. The whole of the investing substance may be thus removed, and the Alga disclosed without any breaking up of its filaments or injury to its cells. In other respects the ordinary methods of microscopical examination are sufficient.

In considering the economic uses of seaweeds, the indirect service they render as the basis of the nutrition of animal life in the sea, and consequently their fundamental importance for fishery, must not be left out of account here, as it practically has been by fishery boards and others whose main concern it might appear to be. In investigating the food of fishes, the so-called practical inquirer is accustomed to look no further than the immediate organisms eaten, much as if in agricultural matters no heed were given to the pasturage of farm stock. There is no doubt that the enormous shoals of *Peridinieæ* and other allied free-floating Algæ are the pastures on which the organisms constituting the food of fishes themselves feed—that in fishery matters they are the basis of the pyramid of which man is the apex, and the dearth of knowledge of these forms and the indifference of fishery authorities to the subject in its technical aspect, is only equalled by the ignorance and apathy of botanists towards its scientific value.

The direct economic importance of Algæ is no longer so great as it was early in the present century, when the kelp industry flourished in the north of Scotland and the western coasts of Scotland and Ireland. The value of kelp in the manufacture of soap and glass became greatly enhanced by the

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exclusion of barilla as an import from our markets during the long war. The price of kelp then rose so high that the income of the Outer Hebrides from this source alone was computed to have reached £120,000 a year. The industry practically came to an end with the peace and the reintroduction of barilla, while the removal of the salt duty struck a further blow at the revenue of these districts. Kelp is now used only in the manufacture of iodine, and as a manure. The common sea-wrack or bladder-wrack (*Fucus vesiculosus*) has been used medicinally for a variety of diseases, but its reputation in this respect has been acquired principally as a remedy for obesity. Bentley and Trimen (*Medicinal Plants*, vol. iv. p. 304) state that "farther trials are necessary before any definite conclusions can be arrived at on its action, and its value as a remedy in obesity. It would appear that it is the essential constituent in the nostrum now so extensively advertised under the name of Anti-Fat." As a food, or rather as a sauce, the species of *Porphyra* known as Laver are not sufficiently appreciated. Laver is not only abundant, but is easily preserved. Carragheen, sometimes called Irish Moss (*Chondrus crispus*), is used for its nutritive properties, which however appear to have been over-valued. Dulse (*Rhodymenia palmata*) and tangles (*Alaria esculenta*) are eaten by the hardy, but are extremely indigestible. The Chinese and Japanese engage in an extensive industry in seaweed products, and certain species are cultivated. Ceylon Moss, or Jaffna Moss (*Gracilaria lichenoides*), a seaweed which abounds in Eastern seas, is the source of Agar-Agar,

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so useful in the preparation of culture-media for observing the growth of bacteria. The same species together with another (*Gracilaria confervoides*, and probably also species of *Eucheuma*) are used by the Chinese and Japanese for making jellies and sweetmeats, and for stiffening purposes, varnishes, &c.

The extensive deposits of fossil Diatoms which occur in several quarters of the world furnish in some cases valuable polishing powders, and are used, as in the case of the Hanoverian Kieselguhr deposit, for mixture with nitroglycerine to form dynamite.

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PLATE I.

1. PELVETIA CANALICULATA.
2. HALIDRYS SILIQUOSA.
3. CYSTOSEIRA ERICOIDES.
4. CUTLERIA MULTIFIDA.

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SUB-CLASS I

PHÆOPHYCEÆ

WITH the exception of some of the species of *Lithoderma* and the genus *Pleurocladia*, represented only by a minute form of doubtful affinity discovered by Alexander Braun in the Tegeler See near Berlin, all the *Phæophyceæ*, or *Melanophyceæ* as they are otherwise called, are seaweeds. They agree in the fact that all their motile reproductive cells, zoospores, antherozoids, and gametes are provided with two lateral cilia, one pointed forwards and the other backwards in motion; in the fertilisation of their oospheres and the conjugation of gametes outside the parent plant, and the direct germination of the zygote which is the product of this union; in the possession of brown chromatophores tinged with phycophæine and phycoxanthine (the phycophæine being soluble in water and the phycoxanthine in alcohol, the compound pigment being termed phæophyll); and in having mostly but one nucleus in the vegetative cells. The vegetative body of the plants coming under this sub-class is of great diversity, including the most highly organised of all seaweeds, of giant dimensions and

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great external differentiation of form and considerable internal differentiation of tissue, as well as others consisting of a mere row or plate of similar cells. The sub-class may be regarded as a fairly natural assemblage of orders easily to be distinguished from the other sub-classes, though it includes such diverse types as (1) the *Fucaceæ*, of which the unciliated oospheres, many thousand times greater than the antherozoids, are produced like the latter in definite conceptacles, from which they are extruded; (2) the *Cutleriaceæ*, possessing non-sexual zoospores, and ciliated oospheres (or ♀ gametes) many times larger than the antherozoids (or ♂ gametes)—the oospheres, however, being incapable of fertile union until they have come to rest—neither borne in conceptacles; and (3) other orders possessing ciliated gametes of equal or nearly equal size, in one case (*Splachnidiaceæ*) borne in conceptacles, in the others within external mother-cells.

It would be doing violence to a natural system of classification to accept the proposed inclusion of the *Diatomaceæ* among the *Phæophyceæ* on the sole ground of colour. This order is of a distinctly aberrant character, and shows no morphological point of contact with even the lowest groups of *Phæophyceæ*.

FUCACEÆ.

General Characters.—The distinctive characters of the *Fucaceæ* are the production of unciliated oospheres in oogonia and antherozoids in antheridia,

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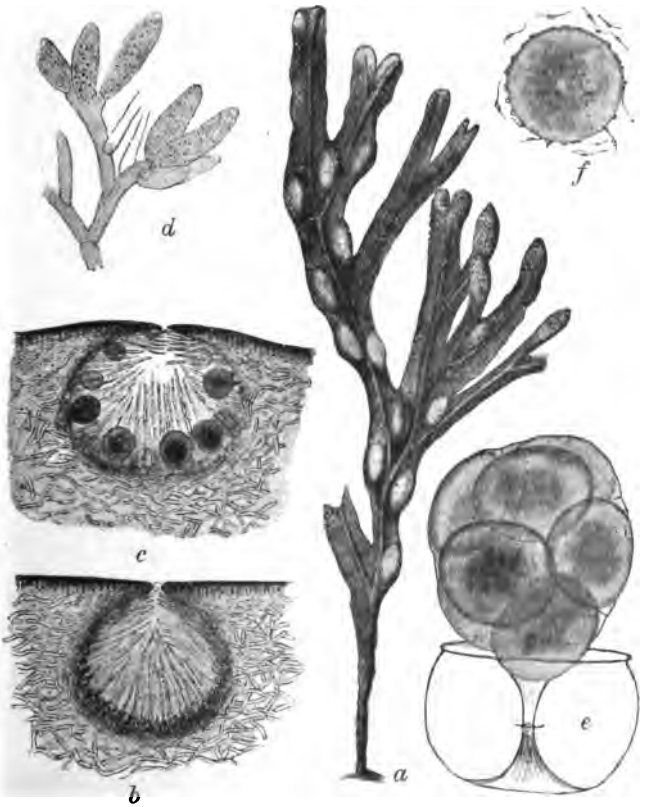


FIG. 2.—*a*, Plant of ***Fucus vesiculosus***, with air vesicles and fertile tips of frond reduced; *b*, male conceptacle of ***F. serratus***; *c*, female conceptacle; *d*, antheridia; *e*, oogonium emerging from outer membrane; *f*, oosphere, with antherozoids. *b*, *c*, *d*, *e*, and *f* highly magnified. (After Thuret and Bornet.)

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both within definite conceptacles more or less localised on the thallus, the oospheres being enormously greater in volume than the antherozoids. The antherozoids are at most sixty-four in each antheridium, while the oospheres are typically eight in each oogonium. In particular genera each oogonium develops only one, or two, or four oospheres, but in all the *Fucaceæ* that have been examined in this respect the original nucleus of the oogonium always divides into eight daughter-nuclei, of which only those remain effective that are destined to belong to oospheres, while the remainder, in genera possessing one, two, or four oospheres, are rejected. Both antherozoids and oospheres are extruded from the conceptacles, and fertilisation takes place, as in the rest of the *Phæophyceæ*, outside the plant. There are no non-sexual spores produced, and with the exception of vegetative propagation by broken off fronds, there is no other kind of reproduction known in *Fucaceæ*. It is probable that in the parasitic and much reduced *Notheia*, of which research has failed to disclose the antheridia, the oospheres remain unfertilised, and if they reproduce the plant, as is extremely probable, do so parthenogenetically. Of all Algæ they show the highest degree of differentiation of parts, and attain the greatest dimensions, with the single exception of the *Laminariaceæ*. A considerable variation, however, occurs among the different genera in the matter of vegetative development, the least of any being exhibited by *Notheia*.

The Thallus.—The thallus of the *Fucaceæ* sometimes attains a development and differentiation of

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parts which extorts the use of such terms as stem, leaf, and root, however unconventional such an employment of them may appear from the point of view of formal morphology. It has been pointed out, for example, that the transition from the lower to the upper leaves of certain species of *Sargassum*

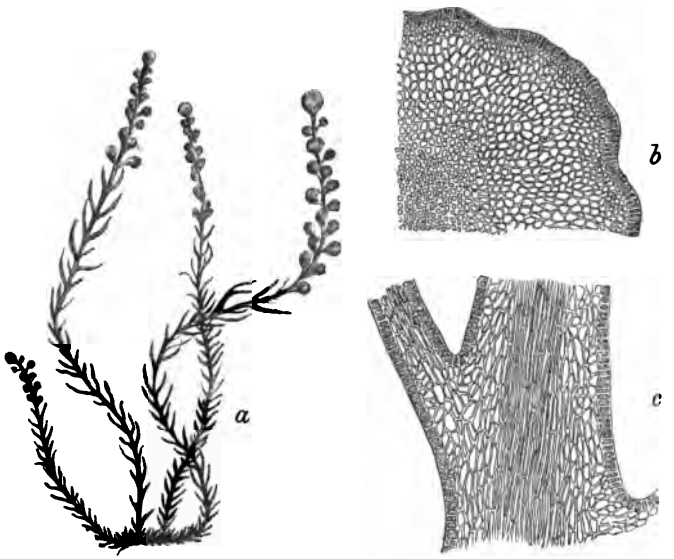


FIG. 3.—*a*, *Coccophora Langsdorfii* (reduced): *b*, transverse section of stem; *c*, longit. section of same passing through base of leaf. *b* and *c* much magnified. (After A. L. Smith, in *Phyc. Mem.*)

furnishes a parallel appearance to the familiar change of form to be observed in the leaves of flowering plants. When such differentiation is allied with the production of special receptacular or fruiting branches, arising from the base of the

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petiole, as exhibited by *Turbinaria, Sargassum,* &c., the appearance of the whole plant (conf. Fig. 7*a*, *b*.) by no means suggests the familiar definition of a thallus. (The strict justification of Prof. Bower's proposal to employ the terms *phyllidium* and *caulidium* when speaking of the oophyte generation in contrast to *phyllome* and *caulome* of the sporophyte, must be admitted, but the advantage of such a usage in morphological argument does not exclude the propriety of employing the more familiar terms when it is expedient.) Greater diversity of appearance is imparted by the transformation of leaves into air-vesicles, formed by a rending apart of the central tissue in young leaves. In this process the fragments of broken-down cells are left behind in the growing cavity, and, at a later stage, the cells bordering the interior form by division a secondary dermal layer. In the mature vesicles a cuticle separates from the internal surface, exposing a layer of large papillate cells. Fig. 7,*g*. The tissues of the higher forms of the *Fucaceæ* are composed of three distinct layers in stem, petiole, and leaf, viz., an epidermal layer of generally narrow, radially elongated cells, and beneath it a band of thick-walled cortical parenchyma passing into a central strand. The epidermal layer is assimilative in its function, and varies in depth from one to several rows of cells. The outermost cells are capable of division, and by this means, dividing radially and tangentially, effect an increase in the thickness of the shoot. A kind of periderm is formed in some *Fucaceæ* by the active division of the outermost parenchyma cells, and may go so far as to represent considerable

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secondary growth in thickness. The central strand of long narrow cells bears a resemblance to the vascular portion of the axis of the higher plants, and continuity of protoplasm has been demonstrated through the pits on the longitudinal walls. This strand is often massively developed in the stem, and traverses the leaf-stalk, where its cell-walls become thinner, into the blade of the leaf, where subdivision of the strand takes place, the subdivisions gradually disappearing and becoming lost in the parenchyma as they approach the edge of the blade. This subdivision frequently begins in the leaf-stalk, but on the other hand the elements of the strand often maintain sufficient coherence to give the appearance of a midrib to the blade. Not only, then, is there a striking external conformation of parts differentiated in these higher forms of the *Fucaceæ*, but the internal structure of the tissues attains a considerable diversity. The mode of branching is either lateral or dichotomous, or even a mixture of both. Most of our British *Fucaceæ* (*e.g.* the genera *Fucus*, *Ascophyllum*, &c.) occupy a lower level of vegetative differentiation, as do also such remarkable genera of the southern seas as *Hormosira*, with its simple, beaded, necklace-like fronds, without lateral foliar expansions or special receptacular branches. In the lowest rank of all comes the quite undifferentiated thallus of such genera as our native *Himanthalia*, resembling a stalked button, from which, however, long dichotomous receptacular branches spring.

The attachment of the thallus to the substratum is most frequently effected by means of a sucker-like

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FIG. 4.—*Himanthalia lorea*, showing the button-shaped thallus and long ichotomous fertile receptacle. Reduced.

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disc, more rarely (as in *Turbinaria*, *Phyllospora*, &c.) by root-like fibres (haptera), and in the case of *Notheia*, by a haustorium, which it drives into the thallus of its host (*Hormosira*, and rarely *Fucodium*), much in the fashion of parasitic flowering plants.

The apical cell, by which growth in length is effected, is generally situated at the bottom of a

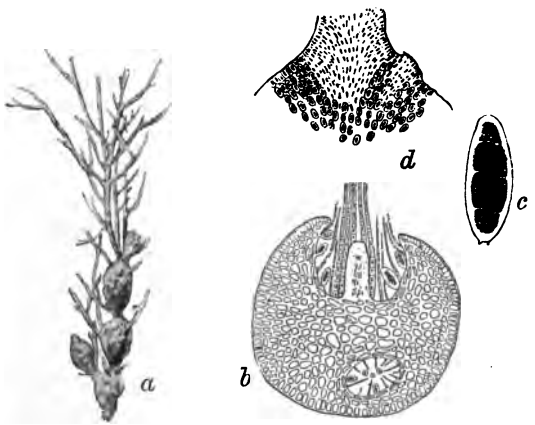


FIG. 5.—*a*, *Notheia anomala* growing on *Hormosira*, half natural size; *b*, section of *Notheia*, showing origin of lateral branch from the base of a conceptacle; *c*, oogonium; *d*, section of junction of *Notheia* with *Hormosira*. *b*, *c*, and *d* highly magnified. (After M. O. Mitchell, in *Phyc. Mem.*)

dimple in the surrounding tissue, and both three- and four-sided cells occur in different genera. Oltmanns, in his classification of the genera of this order, attaches an importance to this three- or four-sided character which is hardly justified by its proved inconstancy in less plastic forms than those of Algæ.

The occurrence of air-vesicles is not characteristic of particular genera, and hardly even of species,

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since varieties of ordinarily vesicular species are known to occur without such floats. In some genera (*Halidrys, Sargassum*, and its allies) they occur in definite positions, but in other genera capriciously, and may be derived from parts of the stem as well as from the leaves. Rosanoff states that they contain nitrogen, while more recent research (Wille, *loc. cit.*) adds oxygen, and denies the presence of carbonic acid.

The reproductive organs of the *Fucaceæ* occur on specialised branches in the most highly differentiated forms, such as *Turbinaria, Sargassum*, &c., and again in one of the least developed in a vegetative sense, viz. *Himanthalia*, which from an insignificant button-shaped thallus sends forth fertile branches several feet in length. They are sometimes to be found (*e.g. Coccophora*) on the air-vesicles only, or on them as well as elsewhere. Frequently they are confined to the thickened ends of leaves or branches (*e.g. Fucus*, &c.) and more rarely (*Durvillea, Sarcophycus*) scattered indiscriminately over large portions of the thallus, or as in *Myriodesma* over the whole thallus, except the root-disc. All degrees are represented, from the highest, imparting to the shoot the appearance of an inflorescence, to the simplest, in which no part is differentiated for the bearing of reproductive organs.

The reproductive organs are borne in conceptacles, which are more or less globular or ellipsoidal cavities situated beneath the surface of the tissue, and communicating with the outside through a narrow opening, the ostiole. These cavities originate near a

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growing-point by the decay or arrest of one or more cells, members of a linear series, which occupy a central position in relation to the changes that follow. By this local cessation of growth and the active division of the adjoining cells there is formed, first a short cylindrical canal, and ultimately the flask-shaped or globular cavity. The initial cell either disappears altogether (as in *Himanthalia*), or only the upper portion (as in *Halidrys*), in which case the middle part gives rise to a hair, while the basal cells share in the formation of the base of the conceptacle. In *Ascophyllum* the whole initial cell persists and subsequently grows out into the conceptacle forming a sort of placenta. In *Notheia*, the branches issue from the base of conceptacles (Fig. 5 *b*), probably owing to the continued development of the initial cell.

Both hermaphrodite and unisexual conceptacles occur. In those cases in which both oogonia and antheridia are borne within the same conceptacle the oogonia usually occupy the base while the antheridia occur on the sides, but this rule is not constant, and they sometimes occur intermixed. When the conceptacles are unisexual it is usually the case that the different sexes occur on different plants, but not always so, as is sometimes asserted.

The oogonia originate from two-celled hairs, the lower of which becomes the pedicel and the upper the oogonium proper. The pedicel cell is usually very short, and in some cases is wholly buried in the wall of the conceptacle. While this is the rule, an exception occurs in *Sarcophycus*, which possesses

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oogonia developed in the usual manner and also others borne laterally on branching filaments. As stated above, the typical number of oospheres is eight in each oogonium, but it is characteristic of different

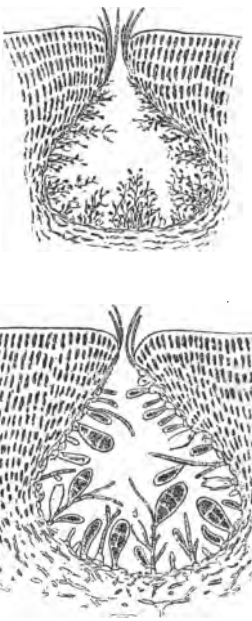


FIG. 6.—*Sarcophycus potatorum*. *a*, section of male conceptacle; *b*, female ditto, both highly magnified. (After F. G. Whitting, in *Phyc. Mem.*)

genera to possess four, two, or only one, though in the latter cases eight daughter-nuclei are formed from the parent nucleus, the appropriate residuum being rejected. The oogonia are usually more or less egg-shaped, varying towards a globular form on

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the one hand and a somewhat elongated shape on the other. When eight oospheres are rounded off there are usually two at the top, four in the middle, and two at the bottom, but in the elongated oogonium of *Notheia* there is one each at top and bottom and two groups of three between. When four oospheres are formed, three usually occupy the base with one above, but it also happens (*e.g. Sarcophycus*) that the protoplasm divides into three transversely and the middle portion afterwards into two longitudinally. In cases of two, the one is placed above the other.

When the outer wall of the oogonium bursts, the rounding of the oospheres is soon completed and they are extruded together, still within the inner wall, which either bursts in turn or appears to dissolve, setting free the oospheres into the surrounding water. In *Pelvetia*, however, the gelatinous wall persists without apparently proving an obstacle to fertilisation.

The antheridia occur as the terminal cells of branches of much-branched hairs. They are generally of a longish oval form and are produced in great abundance. The antherozoids have each two lateral cilia emerging near the apex, and a red pigment spot. In some genera they do not escape forthwith as individuals, but, like the oospheres, pass out of the conceptacle enveloped within the inner wall of the parent cell, while in others they are at once set free so far as this membrane is concerned, but remain close together in a mass until they emerge from the conceptacle.

The paraphyses of the *Fucaceæ* are unbranched, and those near the ostiole frequently protrude. Whether they guide the oospheres and antherozoids outwards,

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or serve as a repellant towards intrusive organisms, or do both things besides discharging other functions is not clear. The liberation of both oospheres and antherozoids takes place on the ebb-tide in the case of those plants that live between tide-marks, probably as a result of relief from pressure. The return of the tide sets all afloat and enables fertilisation to be effected. The round oospheres are many thousand times of greater volume than the antherozoids, and so far as is known are capable of impregnation at any point. Whether this is effected by one or more antherozoids has not been established, and there is a conflict of both observation and analogy on the point. The fertilised zygote becomes encysted within a cellulose membrane, but in the cases observed is capable of germination without the intervention of a period of rest. On germinating the zygote becomes pear-shaped, and the more pointed end is destined to produce the root-portion of the future thallus, while the upper by repeated cell-divisions gives rise to the tissue-system of the thallus. When the young plant is about a millimetre in length a tuft of hairs appears at the apical dimple. Observations of sufficient exactness are wanting of the stages of development that intervene between this one and a later stage at which the young plant has come to assume a more definite or even characteristic form.

Besides the fertile conceptacles there occur in many *Fucaceæ* others that remain barren. They originate in precisely the same manner as the fertile conceptacles, and various speculations as to their significance have been hazarded. They are termed *cryptostomata ;*

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"sterile," "neutral," and "vegetative" conceptacles; *fasergrübchen* by the Germans, and *cryptespilifères* by the French. They are regarded by some as incomplete sexual conceptacles, while others think that

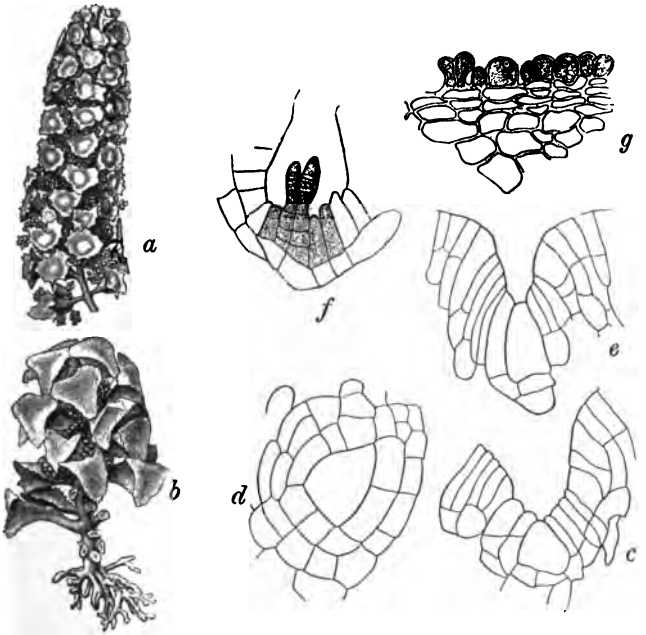


FIG. 7.—*a*, *Turbinaria conoides* (half natural size); *b*, *T. Murrayana*, ditto; *c* and *e*, longitudinal sections of apex; *d*, transverse section of ditto; *f*, young cryptostoma with hairs; *g*, papillate layer lining inner surface of vesicle; *c*, *d*, *e*, *f*, *g*, all highly magnified. (After E. S. Barton.)

the fertile conceptacles are merely cryptostomata that have in time come to bear organs of reproduction. A third view of their significance is involved in the contention that neither form is a develop-

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ment of the other. They contain paraphyses only, which are generally of great length and protrude through the ostiole. Observations are desirable on the paraphyses of both fertile conceptacles and cryptostomata, since it is probable that minute parasitic Algæ have sometimes been mistaken for them. There is, moreover, a difference according to descriptions in their mode of growth *e.g.*; it appears to be acropetal in the cryptostomata of *Cystoseira* and basipetal in those of *Turbinaria*. Since similar cryptostomata of varying shapes, dimensions, and modes of origin occur in the *Laminariaceæ* (*e.g. Saccorhiza, Adenocystis*) and in other *Phæophyceæ*, such as *Chnoospora, Hydroclathrus*, and *Scytothamnus*, any discussion of their nature must involve the consideration of these forms as well as the conceptacles of peculiar origin in *Splachnidiaceæ* bearing non-sexual sporangia.

Thuret has made some interesting experiments on hybridity among *Fucaceæ* and other Algæ—such experiments being much facilitated by the fact that impregnation takes place outside the plant. Experiments with different genera (*Fucus, Himanthalia, Ascophyllum*) were unsuccessful, but he obtained a hybrid between *Fucus vesiculosus* ♀ and *Fucus serratus* ♂, although *Fucus vesiculosus* ♂ could not fertilise *Fucus serratus* ♀. That natural hybrids occur between these species seems highly probable to those who have examined large series of specimens and have observed especially the variation of *F. vesiculosus*. It must not be forgotten, however, that circumstances of environment, such as growth in

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currents, &c., play a very important part in producing mere growth forms which abound in common species like *F. vesiculosus*.

Geographical Distribution.—The *Fucaceæ* occur in all seas, those of the north temperate and arctic regions differing considerably from those of the south temperate and antarctic. Each possesses peculiar types, while the intervening tropical zone has also its characteristic genera. The south temperate zone is richer in generic types than any other region, while the tropical zone (especially the south sub-tropical) with comparatively few genera furnishes the most species. Among the southern temperate generic types with few species there are *Durvillea*, *Sarcophycus*, *Myriodesma*, *Carpoglossum*, *Hormosira*, *Marginaria*, *Scytothalia*, *Carpophyllum*, *Landsburghia*, *Xiphophora*, and *Phyllospora*. Of small genera represented in both northern and southern temperate zones there are only *Pycnophycus* and *Halidrys*. The peculiarly northern genera are *Himanthalia*, *Ascophyllum*, *Pelvetia*, *Egregia*, *Coccophora*, and *Fucus*. (*F. vesiculosus* has been recorded from the Cape and Australia, but the record is open to question.) *Cystophora* has a remarkable distribution, its twenty or more species being limited to warm Australian seas. *Sargassum*, which reaches its maximum in the same region, contains about 150 species, but of a more distinctly tropical character than *Cystophora*. *Cystophyllum* has ten species, mostly sub-tropical, while *Cystoseira*, with thirty species, has a wider range into temperate seas. *Turbinaria*, with a few species, is strictly tropical.

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CUTLERIACEÆ

General Characters.—The reproductive organs of the *Cutleriaceæ* are not borne in conceptacles as in the *Fucaceæ*, but occur in clusters or sori among paraphyses on the outer surface of the plant. The oospheres are ciliated like the antherozoids, which they greatly surpass in size. Fertilisation is not effected until the oosphere has come to rest. There is also reproduction by non-sexual zoospores, intermediate in size between oospheres and antherozoids, and produced in unilocular zoosporangia, also superficial in situation. The growth of the thallus is trichothallic, and in *Zanardinia* the old fronds give rise vegetatively to new individuals by trichothallic gemmæ. The order is a small one, consisting of the genera *Cutleria* (including *Aglaozonia*) and *Zanardinia*.

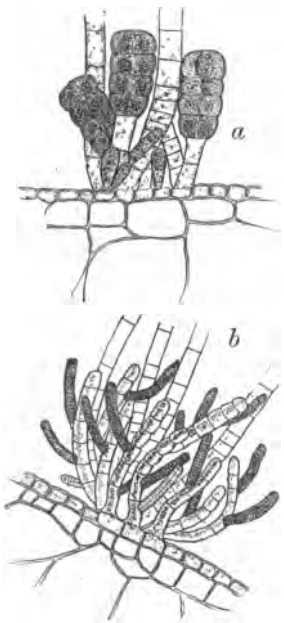


FIG. 8.—*Cutleria multifida*. *a*, female sorus; *b*, male ditto highly magnified.

The *Thallus* in both genera (exclusive of the non-sexual generation of *Cutleria* = *Aglaozonia*) is of

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much the same anatomical structure though of different habit. *Cutleria* grows erect with flat bilateral dichotomous fronds, while *Zanardinia* is resupinate and attached by root-hairs on the under surface. *Cutleria* possesses a thallus composed of three parenchymatous tissues, viz. an epidermal layer of small cells with many chromatophores, a cortical layer of larger isodiametrical cells with few chromatophores, and an axial layer of large cells—the greatest diameter being in the direction of the axis—which are almost colourless. The dorsi-ventral thallus of *Zanardinia* has an upper layer of cells with many chromatophores, and a basal layer of one row of colourless cells producing in many cases root-hairs. The growth of the thallus is tricho-thallic, viz. by means of ultimate hairs, each with an intercalary growing-point, producing outwards a row of cells forming hairs that die off at the apices, and inwards another row which at a short distance below the growing-point unites with neighbouring rows to form a compact thallus. These hairs are in several layers, and their products are traceable for a short distance as definite rows of cells before they become merged in the general tissue-system of the thallus. Lateral extension of the thallus is effected by the branching of these hairs, and subsequent cell-divisions in the superficial cells bring about the formation of the epidermal layer. In the *Aglaozonia* (= reputed non-sexual generation of *Cutleria*) the growth of the thallus is not trichothallic, but by means of marginal initials which by periclinal and radial division produce a

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creeping dorsi-ventral thallus wholly unlike the upright *Cutleria* form. The hairs of the sterile portions of the thallus of the *Cutleriaceæ* grow by transverse divisions of any of the cells and contain chromatophores, while the root-hairs divide only at their apical cells.

The Reproductive Organs.—These originate from single epidermal cells and occur in *Cutleria* on both sides of the thallus, and in *Zanardinia* on the upper surface only. The oogonia and antheridia are borne laterally on tufts or sori of hairs originating as described, and consist of densely compacted tiers of superimposed cells (four cells to a tier in the oogonia and two in the antheridia), those producing the oogonia being considerably larger than the others. Each cell opens by a lateral hole, and in the case of the oogonia produces one oosphere, of the antheridia two antherozoids. Both kinds are biciliated, the oospheres much larger than the antherozoids, and it is not until the former have come to rest that impregnation is effected. Experiments in effecting hybridity between *Cutleria multifida* and *C. adspersa* were wholly negative, the antherozoids being unattracted by the oospheres; while observations of fertilisation within the species have determined a definite attraction by the resting oosphere towards antherozoids for some distance around it. Parthenogenesis is said to occur.

The non-sexual zoospores of *Zanardinia* are produced in unilocular sporangia, elongated and slightly clavate as a rule, standing in dense rows side by side and opening at the apex. Four to six zoospores are

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emitted by each sporangium. While the thallus that bears these sporangia in *Zanardinia* is of the same structure as that which bears the antheridia and oogonia, it is otherwise, as has been said, in *Cutleria*. The young plants produced by the germinating zygote of *Cutleria* are wholly different from the upright thallus of the sexual generation, and these young plants have always proved sterile so far as cultivated specimens directly observed are concerned; but they apparently agree so well with the plants formerly known as species of *Aglaozonia* which do bear zoosporangia like those of *Zanardinia*, that it may be fairly concluded there is an alternation of generations between the sexual *Cutleria* plants which never bear zoosporangia and the non-sexual *Aglaozonia* plants.

There is a resemblance between the sori of antheridia and oogonia in *Cutleriaceæ* and the sori of similar organs in *Fucaceæ*, situated though these are in conceptacles. Sometimes the oogonia of the *Cutleriaceæ* are terminal on unbranched hairs, while the antheridia are, at least those in the middle of the sori, more copiously branched. The oogonia on branching hairs in *Sarcophycus* may be recalled for comparison, while the paraphyses in both orders are not unlike in many respects. The *Cutleriaceæ* are unique, however, so far as is known, in the possession of ciliated oospheres of greater size than the antherozoids (cf. *Codiaceæ*), but otherwise resembling them, and this cardinal fact points to relationship on the other hand with the orders of *Phæophyceæ* in which the gametes are both motile,

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but of equal size and susceptibility to conjugation during motility.

This small order is of limited geographical range. *Zanardinia collaris*, the only species of the genus, occurs in the warm Atlantic (Europe and America) and in the Mediterranean, while the few species of *Cutleria* have a wider range north and south, *C. multifida* being a native of the North Atlantic as far north as Britain and Scandinavia.

DICTYOTACEÆ.

General Characters.—The *Dictyotaceæ* resemble the *Cutleriaceæ* in the non-conceptacular nature of the reproductive organs, and in these being of three sorts—female, male, and non-sexual. Paraphyses occur on the thallus, though not directly in association with the reproductive organs. While all the reproductive bodies of the *Cutleriaceæ* are ciliated, those of the *Dictyotaceæ* are all unciliated. No observation of fertilisation has been made in the case of the bodies presumed to be male and female, and this character is ascribed to them on comparative grounds. The growth of the thallus, which in general habit resembles that of the *Cutleriaceæ*, is not trichothallic, but by an apical cell (*Dictyota*) and by groups of equivalent meristematic cells in the other genera, although in their earlier stages *Taonia* and *Dictyopteris* at least have, like *Dictyota*, an apical cell.

The Thallus of *Dictyota*, *Zonaria*, *Taonia*,

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PLATE II.

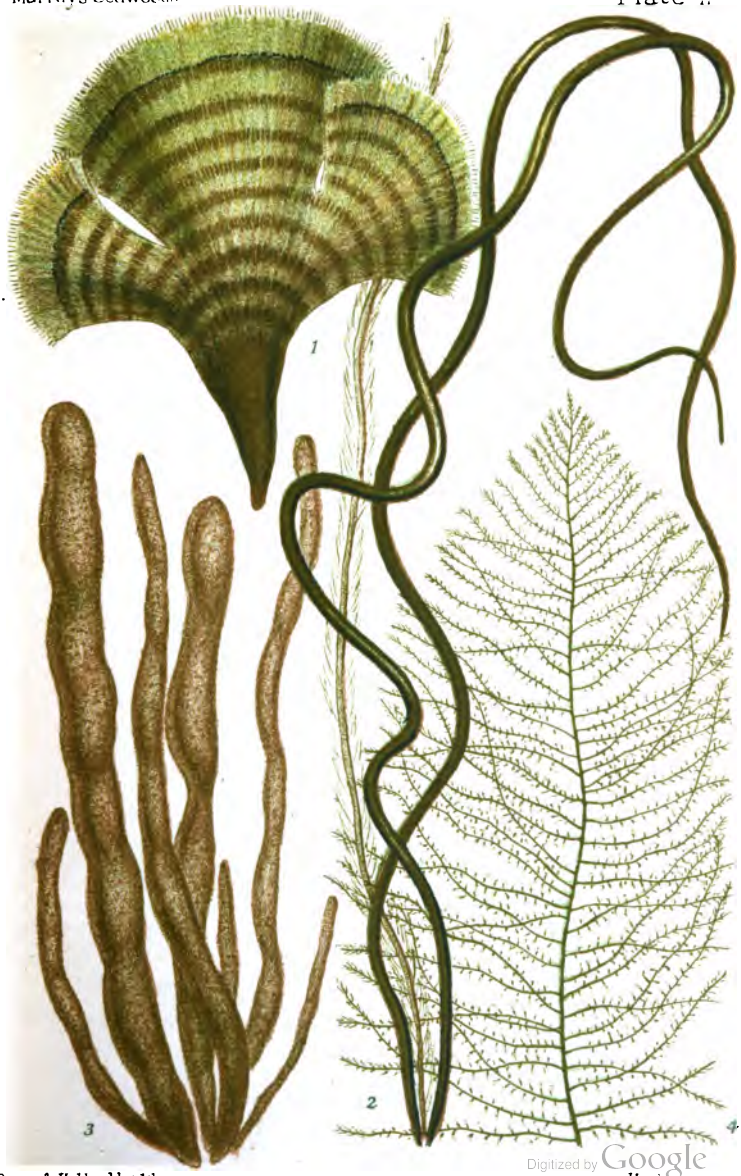
1. PADINA PAVONIA.

2. CHORDA FILUM.

3. ASPEROCOCCUS ECHINATUS.

4. SPOROCHNUS PEDUNCULATUS.

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Stœchospermum, and *Spatoglossum* is erect, flat and frondose, dichotomously branched, and attached at the base to the substratum by root-hairs. In several species of *Zonaria* the frond is procumbent and on its lower surface attached at many points by root-hairs to the surface. *Padina* has a procumbent thallus, but in its ultimate parts assumes a tendency to the upright habit. *Dictyopteris* alone has a mid-rib. The dichotomy of *Dictyota* follows the longitudinal division of the apical cell, while in the other genera the meristematic group divides into two at the point of divergence. The external layers, by repeated transverse and longitudinal divisions, develop an epidermis of numerous small cells, rich in chromatophores, while the internal cells remain large and almost colourless and undergo rare and irregular division. The paraphyses have a basal growth, and occur in tufts or in rows in symmetrical fashion.

The Reproductive Organs occur always on peculiar individual plants. In *Dictyota* and *Taonia* the plants are unisexual; in *Padina* both oogonia and antheridia occur on the same plant; while in all cases the non-sexual spores occur on plants which do not bear other reproductive organs. All three kinds of reproductive bodies are of similar origin. An epidermal cell becomes enlarged and projects slightly, then divides transversely, the upper portion being the mother-cell of the reproductive body, while the lower remains part of the vegetative body. The organs designated oogonia are united in a dense sorus of such cells as have been described, the contents of the reproductive cells remaining undivided

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and being ultimately extruded, each as a motionless oosphere. The antheridia likewise occur in sori, while in *Dictyota* the adjacent epidermal cells develop an envelope surrounding each sorus of

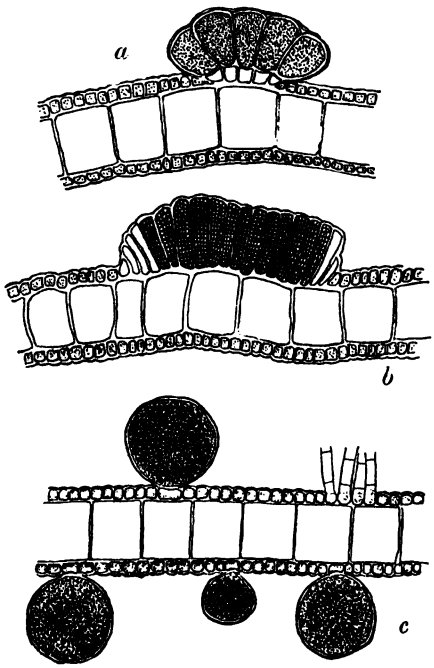


FIG. 9.—*Dictyota dichotoma*; *a*, female sorus; *b*, male ditto; *c*, sporangia; all highly magnified.

antheridia laterally. The contents, after repeated bipartitions into numerous cells, become transformed into a large number of colourless, motionless, unciliated antherozoids, globular or slightly elongated,

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and are set free by the dissolution of the cell-walls. The sporangia occur in clusters in *Padina* and *Taonia*, and in scattered fashion in *Dictyota*. The prevailing number of spores is four, but frequently only two, or rarely one. The division into four is either simultaneous, when the resulting arrangement is that of a tetrad, or by two successive bipartitions, when the four spores lie in one plane. The spores escape by an apical opening of the sporangial wall, are motionless, and at first without a membrane. They soon, however, secrete a cell-wall and germinate. The process of germination, so far as it has been observed, is the same for spores and oospores, but the product of germination is either directly (*Dictyota* and *Zonaria*) a small plantlet of the parent form, or (*Padina*, *Taonia*, and *Dictyopteris*) a protonema-like body from the superficial cells of which one or more shoots arise in the form of the parent plant.

None of the *Phæophyceæ* have caused greater diversity of opinion as to their relationship than the *Dictyotaceæ*. Some authors have gone so far as to place them with the *Florideæ* or in a position apart from the *Phæophyceæ* but pointing towards the *Florideæ*, and this indeed appears to be the favourite view of their character, especially with those who demand a link between *Phæophyceæ* and *Florideæ* (though such a link might perhaps better be sought lower in the scale than the *Dictyotaceæ*). This opinion is based on the unciliated character of all the reproductive bodies, the resemblance of the motionless antherozoids to the pollinoids of *Florideæ*, and the division into four of the spores constituting

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a likeness to the tetraspores of the same group. Many authors, in fact, describe unhesitatingly both these bodies by the terms appropriate to *Florideæ*. The contention rests on no more than this slender support and the suggestive influence of the employment of such terms as tetraspores, &c., for the *Dictyotaceæ*. The absence of any observation of fertilisation leaves the field open for such speculation. On the other hand, no trichogyne has been observed, and the presumptive female reproductive organs suggest degeneration from *Phæophyceæ* very much more than affinity with *Florideæ*. The antheridia, apart from the motionless character of the antherozoids, correspond better with similar bodies among the *Phæophyceæ*, and the envelope enclosing the sorus in *Dictyota*, while morphologically not directly comparable with a conceptacle, yet resembles it as much as it does any corresponding body in the *Florideæ*. The fancied resemblance to tetraspores attributed to the non-sexual spores is based merely on their number, though this is inconstant (as it is, however, among the *Florideæ*). But the spores are extruded without a membrane and their condition is, to say the least, just as consistent with loss of cilia as with loss of membrane—a purely physiological condition scarcely admissible in such an argument. The vegetative organs are overwhelmingly in favour of their character as *Phæophyceæ*. If we take the *Cutleriaceæ*, in which the mode of thallus development is different, as has been described, we see all three sorts of reproductive bodies ciliated, while in *Dictyotaceæ* all three are motionless.

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But the absence of cilia is not confined to this order. In the *Fucaceæ* the oospheres are motionless. In the *Tilopteridaceæ* the homologous bodies are also motionless, while in the *Ectocarpaceæ*, *Ectocarpus pusillus* produces immobile spores in the plurilocular sporangia. This physiological condition may be misleading when made too much of in a morphological argument. If we disregard it, and take into account the character of the vegetative organs, the balance of evidence points to affinity with the *Phæophyceæ*. It may be objected that the trichothallic growth of *Cutleria* is very different from that of the *Dictyotaceæ*. But it may be recalled that the growth of the *Aglaozonia* or non-sexual forms of *Cutleria* is not trichothallic, but by marginal initials. Again, it would be unwise to lay down a hard and fast rule in this matter when we remember the tuft of hairs at the apical dimple in young *Fucus* plants, for example, which may indicate, as other facts do, that no great gulf separates trichothallic growth from that by an apical cell or group of equivalent initial cells. The *Dictyotaceæ* are placed here next the *Cutleriaceæ* more from contrast than implied affinity. We may compare the three kinds of reproductive bodies, ciliated in the one case, unciliated in the other. Since such loss or absence of cilia occurs elsewhere in the *Phæophyceæ*, it appears to be more reasonable to regard the *Dictyotaceæ* as degenerate members of this group, with motionless reproductive organs occurring in definite sori for the most part as in *Cutleriaceæ*, though not in conceptacular fruits as in *Fucaceæ*.

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The Geographical Distribution of the *Dictyotaceæ* is characteristic of temperate and tropical seas, but reaches its maximum in the warmer waters of the tropics.

TILOPTERIDACEÆ.

General Characters.—This small order is of uncertain position, since the true character of the reproductive organs has not yet been ascertained. These are of two sorts: (1) bodies comparable with the antheridia of the *Cutleriaceæ*; (2) larger unilocular bodies, presumptive oospheres. No process of fertilisation has been observed, and the thallus affords from its morphological character no other clue than the indication of strong agreement with the *Ectocarpaceæ*.

The Thallus in all three genera—viz. *Tilopteris*, *Haplospora*, and *Scaphospora*—takes the form of tufts of more or less branching filaments attached to the substratum by root-hairs. In *Tilopteris* the branches are opposite, and the primary branches bear short secondary ones; while in *Haplospora* and *Scaphospora* the branches are alternate but irregular. The upper portion of each filament always consists of a single row of cells, while the lower consists of tiers of several cells of equal length. Growth in length takes place by intercalary division. The upper ends of the branches are fine and hair-like, the cells becoming longer, and containing little protoplasm and few chromatophores. The cells contain each a large central nucleus with nucleolus, surrounded by

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a protoplasmic layer which is connected by fine threads with the layer lining the wall. The chromatophores vary slightly in shape, being flat discs usually round but frequently elongated.

The Reproductive Organs.—The larger unilocular bodies which occur in all three genera contain but one oosphere each, unprovided with cilia, and having in the

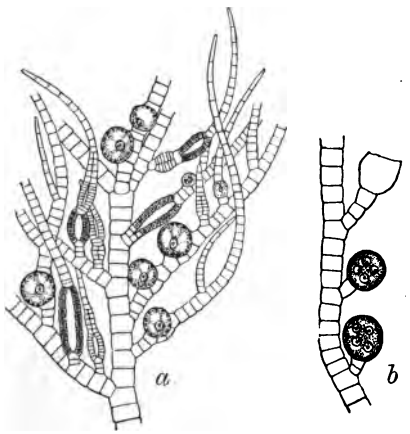


FIG. 10.—*a*, *Scaphospora speciosa*, with antheridia and presumptive oogonia. *b*, *Haplospora globosa*, with presumptive oogonia: highly magnified.

case of *Scaphospora* one nucleus, *Haplospora* four, and *Tilopteris* two or more. In *Tilopteris* and *Haplospora* it is clothed with a membrane before emission, but in *Scaphospora* the wall is not secreted until after it is set free. In *Tilopteris* these bodies are intercalary in the filaments, and occur in pairs or in fours; in *Haplospora* they are shortly stalked; and in *Scaphospora* they are partly immersed in the branches, one of the cells of which acts as a basal cell. If we

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regard these bodies as oogonia, the objection arises that they are set free, in two of the genera, enveloped in a wall; but it may be remembered that the oogonia of *Pelvetia* have a persistent inner gelatinous wall which does not prevent fertilisation. The view is also tenable and more probable that they are parthenogenetic, a condition said to occur occasionally in the *Cutleriaceæ*. The antheridia are known only in *Tilopteris* and *Scaphospora*, and occur usually as intercalary bodies on the branches. They arise by radial and transverse divisions, and are elongated, hollow cylinders composed of tiers of small cells, each of which gives rise to a ciliated antherozoid.

The difficulties of interpretation in the case of these presumptive oogonia and antheridia are much increased by the occurrence of aberrant species in the genus *Ectocarpus*. It must be remembered that the *Ectocarpaceæ* supply the closest parallel to the *Tilopteridaceæ* in respect of the morphology of the thallus. Besides the unilocular and plurilocular sporangia characteristic of *Ectocarpus*, there have been recorded by MM. Thuret and Bornet bodies to which one can have no hesitation in applying the term antheridia. These occur in *E. secundus* and in *E. Lebelii*, and M. Bornet,[1] in recurring to this subject, refers to the grave difficulty it presents to the systematist. The antherozoids completely resemble those of *Fucus*, *Cutleria* and *Tilopteris*, and we must inevitably regard them as possessing the same potentiality. The absence of a chromatophore and of

[1] *Bull. de la Soc. Bot. de France*, Tom. 38, 1891.

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reserve-material in their protoplasmic contents points farther to an incapacity for independent development. The so-called zoospores of these species are almost as much greater than these in size as the ciliated oosphere of *Cutleria* is greater than its antherozoids. Another aberrant species of *Ectocarpus*, viz. *E. pusillus* Griff.,[1] presents a difficulty of another kind. The spores (at least those of the plurilocular sporangia) have no cilia, and are immobile. This latter character does not really point to the *Tilopteridaceæ*, since the unilocular sporangia of *E. pusillus* contain a number of spores, and, as has been seen, the unilocular bodies in *Tilopteridaceæ* have but one spore (or oosphere, as the case may be).

These difficulties primarily concern the classification of *Ectocarpaceæ*, but their occurrence has a special significance to those who desire to interpret similar organs in the *Tilopteridaceæ* and neighbouring groups. M. Bornet is disposed to give the first place in such matters to the morphological characters so strikingly alike in *Ectocarpaceæ* and *Tilopteridaceæ*, and to retain these groups in proximity, pointing out that the unilocular, monosporous sporangia and the form of the antheridia sufficiently distinguish them from the *Ectocarpaceæ*. Whether we have to deal with a unilocular, monosporous sporangium or with an oogonium containing one oosphere in the *Tilopteridaceæ* can only be settled by observation.

This order is known only from the North Atlantic (including Mediterranean) and Arctic Sea. *Tilo-*

[1] Not *E. pusillus* of Kützing, in which Goebel has observed conjugation. The latter is properly called *E. globifer*, as Bornet has shown.

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pteris Mertensii and *Haplospora globosa* have been found in British seas at Cumbrae in the Clyde Sea area.

SPLACHNIDIACEÆ.

General Characters.—The only reproductive organs known in this monotypic order are zoospores contained in sporangia borne within conceptacles resembling in appearance those of the *Fucaceæ*, but originating in a different manner. The sporangia are unilocular and resemble very closely those of the *Laminariaceæ*. The zoospores presumably germinate without conjugation, like the zoospores of other unilocular sporangia in the *Phæophyceæ*, but no observations have as yet been made. The thallus, which is of considerable stature, is attached to the substratum by a disc, and consists externally of parenchymatous cells, and internally of threads traversing a ropy mucous mass. It grows by means of an apical meristem. Only one species is known, viz. *Splachnidium rugosum* Grev.

The Thallus.—Plants of *Splachnidium rugosum* vary from about four inches to a foot in height, and spring in five or six separate fronds from a common disc. Each frond is of cylindrical form, tapering downwards and ending bluntly upwards, while giving off irregularly smaller branches of similar form. It is marked by numerous pits containing hairs, and at a later stage sporangia. The outer wall consists of two layers of epidermal cells, small and approximately cubical in shape, and three layers of cortical cells, at first poly-

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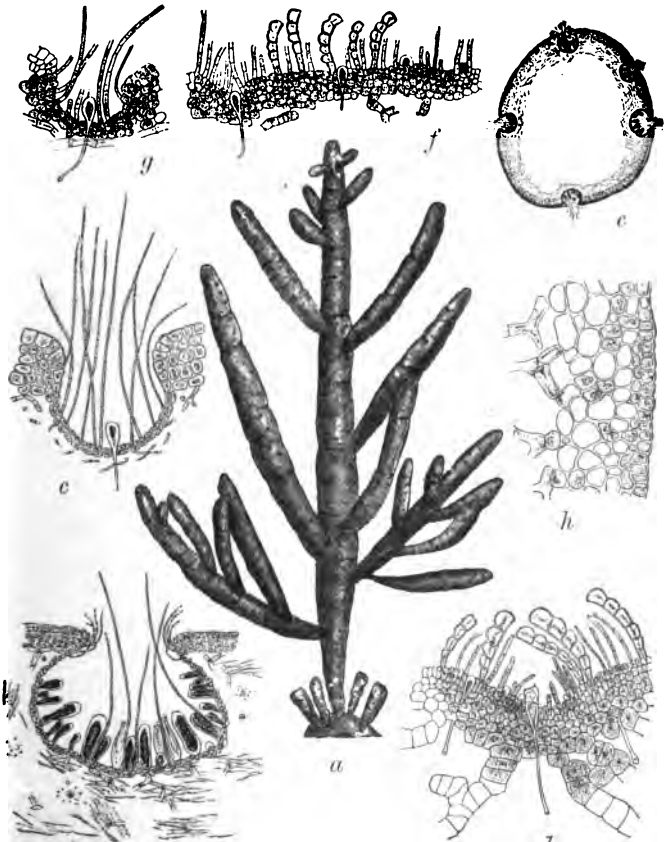


FIG. 11.—*Splachnidium rugosum* Grev. *a*, plant reduced one-half. *b*, section through apex, showing apical cell. *c*, section through young conceptacle. *d*, conceptacle with sporangia. *e*, section through branch. *f*, early stages in the development conceptacles, showing four initial cells. *g*, further stage in development of conceptacle. *h*, transverse section of thallus. *b* to *h* much magnified. (After M. O. Mitchell and F. G. Whitting, in *Phyc. Mem.*)

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gonal, but becoming somewhat ovate by unequal growth. Immediately within these are strands of hyphal filaments giving off smaller branches and traversing the peripheral portion of the mucilaginous mass which fills the interior of the elongated sac-like fronds, and running for the most part in the direction of the axis. The fronds are covered externally with a mucilaginous coating. The young cells of the outer epidermal layer give rise to septate hairs, the upper cells of which frequently become almost spherical or bulge unilaterally, imparting a moniliform appearance. These hairs bend towards the apical cell. Growth takes place as the result of the activity of a group of meristematic cells surrounding an apical cell unique in its character. This apical cell differs entirely from its neighbours in appearance, being larger and pear-shaped, with a thick mucilaginous wall and a long filiform tail stretching towards the interior of the thallus. The apical cell and its surrounding meristem are sunk in a dimple of the tissue. The two outer layers of the meristem by radial division form the epidermal cells, which continue to divide until the part of the thallus in which they lie attains maturity. The inner cells of the meristem form the cortical cells, which, when once formed, do not divide again, but increase in size, and by this means, as well as by separation, keep pace with the growing epidermal layers. The meristematic cells lying internally and immediately round the apical cell give rise to the filaments by tangential division. These branch and anastomose repeatedly, forming a plexus of filaments immediately beneath

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the apex. The apical cell persists throughout life at the ends of the main shoot and branches.

The Reproductive Organs. — Conceptacles are formed by the transformation of one of the young epidermal cells near the apex into an initial cell resembling in all essential points the pear-shaped apical cell. This initial cell is the homologue of the initial cell in the development of the conceptacles of the *Fucaceæ*, but it undergoes no division and no further development. The epidermal cells surrounding it divide and the cortical cells in its neighbourhood increase in size; by a combination of these processes the initial cell is placed at the bottom of a cylindrical depression, while hairs (paraphyses) arise from the youngest epidermal cells with others formed earlier surrounding the mouth. The upper pear-shaped portion of the initial cell stands out prominently from the base. In *Fucus*, on the other hand, a young conceptacle with a small ostiole is formed before the paraphyses appear. The conceptacle enlarges by radial division of the lining cells, and though the base becomes larger than the mouth, the flask-shaped form seen in the *Fucaceæ* does not occur. The paraphyses are long, septate, and unbranched, dividing at the base, and forming tufts which emerge far beyond the mouth. The conceptacles at this stage thus resemble in appearance the cryptostomata of the *Fucaceæ*.

The sporangia, which are unilocular, are formed among these paraphyses as protuberances of the lining cells of the conceptacle. They elongate and enlarge into club-shaped bodies with the base sunk

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among the adjacent cells. There is no division of the original cell into pedicel-cell and sporangium. When the sporangium reaches its full size the contents are simultaneously divided into zoospores, which do not wholly fill the interior. These escape by the rupture of the wall at the apex, and their active motion has been observed by Mr. R. M. Laing. They are from 500 to 600 in number in each sporangium, and are of the same size as the antherozoids of *Fucaceæ* and the zoospores of the *Laminariaceæ*, which latter are formed in similar sporangia. The number of sporangia in each conceptacle increases with age, and they appear to crowd out, as it were, the paraphyses, of which only a few are seen among the sporangia at the base of a mature conceptacle. They remain, however, in considerable numbers surrounding the mouth. The empty sporangia persist, unlike the oogonia of the *Fucaceæ* in a similar situation.

This remarkable plant was included among the *Fucaceæ* until it was placed apart in its present position on its true nature being disclosed by the admirable investigation of Miss Margaret Mitchell and Miss Frances Whitting.[1] Its nearest known allies are undoubtedly the *Laminariaceæ*, from which it differs mainly in the sorus of sporangia being enclosed within a conceptacle and thus definitely limited, and by its remarkable apical cell.

Its geographical range is in the southern ocean, where it is found at the Cape of Good Hope, Australia, New Zealand, Seal Island, &c.

[1] Murray's *Phycological Memoirs*, part i. 1892.

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LAMINARIACEÆ

General Characters.—As in the *Splachnidiaceæ*, the only known reproductive organs are zoospores formed within unilocular sporangia. These occur

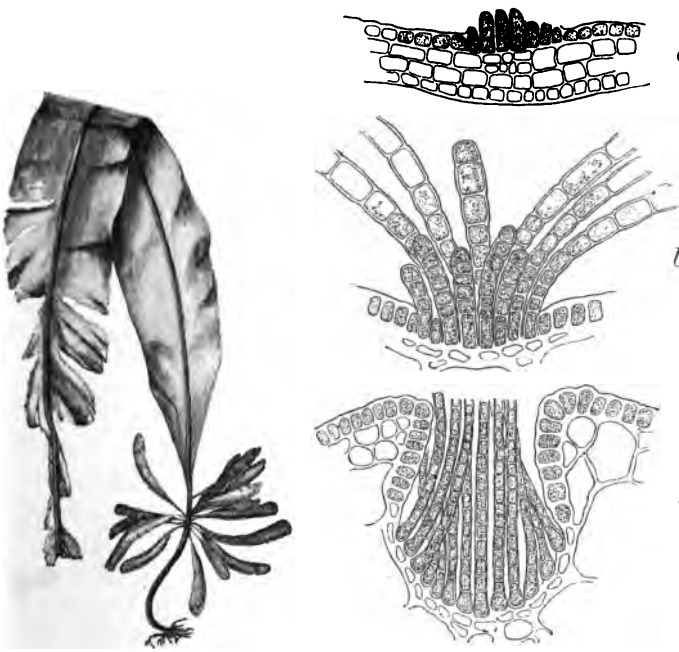


FIG. 12.—*Alaria esculenta*, much reduced. *a* and *b*, tufts of hairs from young frond. *c*, cryptostoma of *Saccorhiza bulbosa*. *a*, *b*, *c*, much magnified.

together with non-septate paraphyses, not within conceptacles, but in sori. Except in the case of *Chorda*, where the sorus covers the whole surface of

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the frond, these sori are more or less localised, though usually of variable and irregular outline. The thallus is in nearly all cases of considerable size, in some of gigantic proportions exceeding in length all other plants (*Macrocystis*) and attaining a girth (*Lessonia*) comparable with that of trees. The brown tangles of our seas are typical representatives of the order. In all cases except *Chorda* there is a differentiation of stalk and blade, and the growing-point, which is an intercalary group of meristematic cells, is situated at their junction. In point of differentiation of the vegetative organs the order rivals the *Fucaceæ*, and generally exceeds it in stature. Cryptostomata with septate paraphyses occur in *Saccorhiza*, *Adenocystis*, and *Ulopteryx*, while tufts of such paraphyses not within cryptostomata are found on the fronds of *Alaria*.

The Thallus.—The order has been divided by Mr. Setchell into three tribes, according to the methods by which the complexity of form of the adult plants is attained. The differences in question naturally arise at the intercalary growing-point, and the three types of growth are the *Laminaria* type, the *Lessonia* type, and the *Alaria* type.

The *Laminaria* type, to which the genera *Chorda*, *Saccorhiza*, *Agarum*, *Thalassiophyllum*, *Costaria*, *Cymathœre*, and *Arthrothamnus* conform, is characterised by unbranched fronds (except *Thalassiophyllum*) and by a simple unmodified plane growing-point situated at the place where the stalk expands into the blade, with nothing in its appearance to the naked eye indicating the fact that here the stalk is

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increasing in length upwards and the blade is growing at its base. The *Lessonia* type, to which the genera *Dictyoneuron*, *Postelsia*, *Nereocystis*, and *Macrocystis* conform, is characterised by greater complexity of fronds, which are branched in all cases except *Dictyoneuron*, and this branching originates in a splitting at the growing-point, causing unequal divisions in *Macrocystis* and equal ones in the other



FIG. 13.—*Laminaria digitata.* Reduced.



FIG. 14.—*Agarum Turneri.* Reduced.

genera. In *Lessonia*, which has numerous blades borne at the ends of the dichotomously branching stalk, and as many growing-points as there are blades, the branching arises in consequence of a longitudinal slit in the middle of the growing-point. This slit in the growing-point at the base of the blade extends, or appears to extend, both upwards and downwards as the blade and the stalk increase

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in length, until at last there are two blades, each with its own short branch and its own growing-point. The primary blade thus has its place taken by those split off from it, and these again and again by others. In *Dictyoneuron*, which is unbranched, the long narrow, veined fronds become divided into two by the splitting at the growing-point, and the fissure extends almost to the base of the stalk, so that little of a common stalk is left. This portion frequently becomes covered with rootlets, so that the ultimate appearance is that of a group of separate plants. The *Alaria* type, to which the genera *Pterygophora*, *Ecklonia*, *Ulopteryx*, *Eisenia*, and *Egregia* conform, also possesses compound fronds; these, however, do not arise by a process of splitting, but by outgrowths from the meristematic cells at the growing-point. In *Alaria* there is a large terminal blade and a simple short stalk with a growing-point in the usual place, but on the upper portion of the stalk there are two rows of leaflets or sporophylls, on which alone the sori of sporangia are borne. These sporophylls arise as outgrowths from the lower region of the meristematic cells constituting the growing-point, and as



FIG. 15.—*Postelsia palmæformis*. Reduced.

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growth proceeds they are left behind, as it were, by the upward advancing growing-point, and by the time they are mature they are situated some distance below it, while new sporophylls are formed successively above them, imparting a pinnate appearance to the frond. In *Ecklonia*, *Ulopteryx*, and *Eisenia* the sporophylls arise at the base of the blade rather than at the tip of the stalk, while in *Egregia* they spring from the entire length of the growing-point, and thus when full-grown are situated on the margins of both blade and stalk.

As the result of the operation of these modes of growth acting in diverse ways the *Laminariaceæ* present a considerable variety of forms. *Chorda*, as has been mentioned, possesses no leaf-blade, but the other genera approaching *Laminaria* itself exhibit great fronds, simple as a rule, but also digitately divided as in *Laminaria digitata*. The most humble form of all is *Adenocystis*, in the southern ocean, a small sac-like, ovate frond on a very short stalk. The fronds of *Agarum* and *Thalassiophyllum* are perforated, and the latter is branched, but the branches do not arise as in *Lessonia*; they are proliferations from the margins of newly formed perforations at the growing-point. There are midribs in the fronds of *Agarum*, *Cymathære*, *Ulopteryx*, and *Alaria*, while *Costaria* has several ribs each confined to its own surface of the frond, three on the one side and two on the other. The blade of *Dictyoneuron* has a network of prominent veins, while *Postelsia* has longitudinally wrinkled blades. *Nereocystis*, *Macrocystis*, and *Egregia* possess air-floats, those of *Nereocystis* being of great

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size. In the last-mentioned genus the stalk is long, slender and solid at the base, but becoming hollow and broader above; near the top it expands into a globular or elongate pear-shaped bladder, bearing

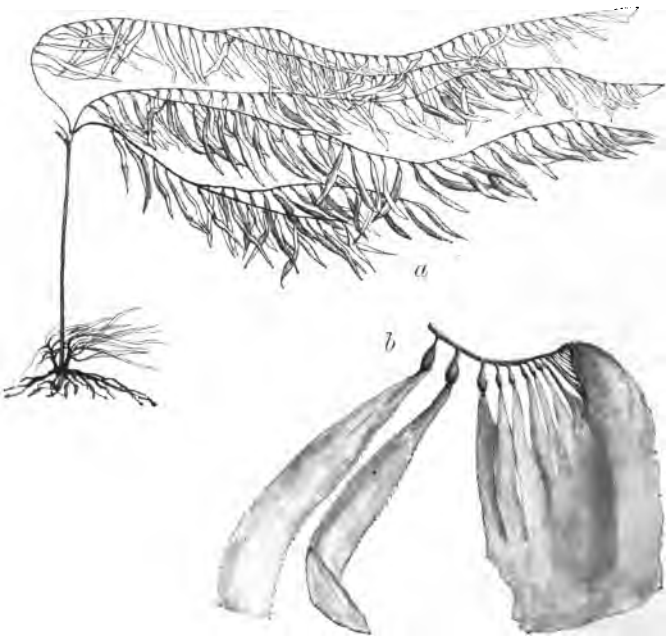


FIG. 16.—*Macrocystis pyrifera*. *a*, diagrammatic sketch of habit, the sporophyllous leaves at base of stem. *b*, apex of frond showing leaves splitting off. Reduced.

two bunches of leaves. In *Macrocystis*, the most gigantic of all the forms, attaining frequently a length greater than that of any other plants and measuring hundreds of feet, the leaves are formed on one side only of a scimitar-shaped blade by parallel

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slits. Its air-floats are pear-shaped, and the power of flotation is so great that large stones to which it grows attached are sometimes wrenched free and thus transported. The greatest girth of stem is attained by *Lessonia*.

The holdfasts are in most cases strong rootlets, but in *Saccorhiza* ("sea-furbelows") whorls of tentacula or haptera are developed after the primary holdfast. These originate immediately above it from a swelling, the rhizogen, which in *S. bulbosa* becomes enlarged into the bulb characteristic of this form.

Several distinct tissues, as might be expected, go to compose the thallus of the *Laminariaceæ* and in this respect their differentiation recalls that of the *Fucaceæ*, while in some respects it surpasses it in degree. The epidermal layer consists of cells slightly elongate in shape and containing chromatophores. It is the assimilative tissue in the leaves and in the stalks as well, though in the latter case it often loses this character and assumes that of a meristematic layer bringing about the secondary growth in thickness of the stalk. However, in other forms this secondary growth in thickness is the function of a special peripheral meristem, which, as in the higher plants, adds centripetally to the thickness of the internal tissues of the stalk and at the same time centrifugally to an external bark-like tissue. Within the epidermal layer there is a parenchymatous layer of thin-walled cells, which composes the greater part of the leaf-tissue and a considerable portion of that of the stalk. Bordering this tissue internally there occurs in the stalks another layer of elongate cells with

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thick, pitted walls, which appears to discharge the special function of a supporting tissue. In *Macrocystis* it is the inner portion of this layer that develops into sieve-tubes, of which the sieve-plates become endued with a callus-like coating. By the periodical addition of such tissues the old stalks of *Laminariaceæ* acquire the appearance of the stems of woody Dicotyledons. Occupying the central portion of the stalk there is a dense plexus of branching anastomosing filaments, which probably acts as a conducting tissue. It is gradually reduced in bulk upwards, and enters the midrib of the leaf, when present, as a thin strand. In several *Laminariaceæ* there are formed definite mucus-passages, mostly in the form of branching anastomosing tubes, and these are frequently bordered by other cells differentiated from those of the adjoining tissues.

The Reproductive Organs are zoospores produced in elongate, sac-like, unilocular sporangia of the same shape as those of the *Splachnidiaceæ*. They occur, as has been mentioned, in more or less localised sori, mixed with paraphyses. On the one hand, in *Chorda*, the sporangia occur over the whole surface; on the other, in *Alaria* and its allies, they are restricted to special sporophylls, as described above. In *Postelsia* and *Macrocystis* the sporangia are borne in the longitudinal furrows in the fronds. The paraphyses, unlike those of *Splachnidium*, are non-septate, and in all cases, except *Saccorhiza* and *Chorda*, possess a peculiar hyaline appendage at the tip. Reinke has placed *Chorda* outside the *Laminariaceæ* on account of its cylindrical thallus and the distribution of its spor-

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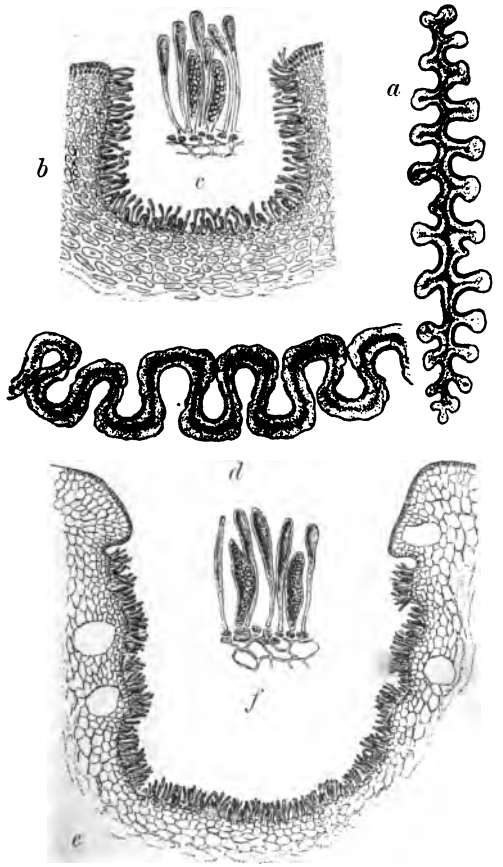


FIG. 17.—*a*, transverse section of leaf of *Postelsia*, showing furrows; *b*, transverse section of furrow with sporangia; *c*, sporangia and paraphyses; *d*, transverse section of frond of *Macrocystis*; *e*, transverse section of a furrow with sporangia; *f*, sporangia and paraphyses. Variously magnified. (After A. L. Smith and F. G. Whitting, in *Phyc. Mem.*)

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angia over the whole surface. He assigns it a place near *Scytosiphon*, which it resembles in habit. These reasons appear to be inadequate when we remember the slightly differentiated thallus of *Adenocystis*, for example, and the further fact that within the *Laminariaceæ* there are various degrees of localisation and restriction of sori. Its paraphyses, which are aberrant, are nevertheless in agreement with those of so typical a Laminarian as *Saccorhiza*. On the whole there appears to be room within the *Lami-*

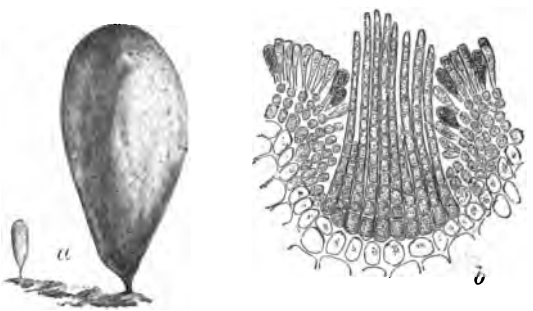


FIG. 18.—*a*, *Adenocystis Lessonii* reduced one-half; *b*, cryptostoma, from centre of sorus of sporangia highly magnified.

nariaceæ for *Chorda*, unless Mr. Buffham's discovery of plurilocular sporangia in association with it should prove to be well established, and not a case of an epiphytic Alga. In that case *Chorda* would have to go.

The cryptostomata with septate paraphyses which occur, as mentioned above, in certain genera resemble in appearance, though not in mode of development, the conceptacles of *Splachnidium*. Only in *Adenocystis*, which in other respects is not unlike *Splachnidium*,

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do these cryptostomata occur in association with the sporangia. In its case the cryptostomata are found on the sporangium-bearing surface, though repeated observations have failed to discover sporangia within the cryptostomata. They stop at the brink of the cavity, and indeed overhang it.

The Geographical Distribution of the order is throughout the temperate and polar seas, being limited by the warm waters on the one hand and the permanent ice on the other. *Laminaria Schinzii* just enters the tropics at Walfisch Bay on the south-west African coast, but within the influence of a cold current. *Laminaria* and its immediate allies are characteristic of the northern seas. *Lessonia* inhabits the Pacific north and south, while *Macrocystis* has an immense range in the southern seas, and in the Pacific up the whole American coast to Alaska and over to the coast of Asia at Kamtschatka. It does not extend up either the African or South American shores of the Atlantic to any extent. The Pacific coast of North America, otherwise rich in *Laminariaceæ*, possesses the peculiar genera *Dictyoneuron*, *Postelsia*, *Nereocystis*, *Cymathære*, *Pterygophora*, *Egregia*, and *Eisenia*, many of them limited to California, and all of them with only one species except *Nereocystis*. Alaska has thirty species, and California, so rich in generic types, has fifteen, but they have only three of them in common. *Ecklonia* occurs in the southern seas and in Japan, while the too numerous species of *Alaria* are all northern. The genera occurring in the British seas are *Laminaria*, *Saccorhiza*, *Alaria*, and *Chorda*.

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SPOROCHNACEÆ.

General Characters.—The sporangia are lateral branches of hairs arising from the superficial cells, and are unilocular. The growth of the thallus is trichothallic, the growing-point being situated in a group of cells at the base of the terminal tuft of hairs. The cells are produced in rows free from each other, but these become united below into a parenchymatous tissue. A thallus of considerable size, diversity and beauty of form is characteristic of the group.

The Thallus, originating as described, is mostly branched on all sides and round or flat in section. The growing branches are crowned each with a tuft of hairs, which falls off on the cessation of growth in length. The parenchymatous cells composing the thallus decrease in size towards the margin, and the more superficial ones contain the bulk of the chromatophores.

The Reproductive Organs occur in sori or on definite fertile portions of the thallus, and the sporangia are lateral branches of the sporangiophores. The sporangia are mostly obovate or elongate-ovate in form, and spring in some cases from the base of the sporangiophores, more frequently at intervals throughout their length. In *Nereia* the sporangiophores occur in sori, and in the other genera—*Sporochnus*, *Carpomitra*, *Bellotia*, *Encyothalia*, and *Perithalia*—definite fertile branches of the thallus are produced, of more or less characteristic forms, those of *Spo-*

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rochnus being usually club-shaped or cylindrical, with a terminal tuft of filaments.

The Geographical Distribution of the *Sporochnaceæ* is mainly confined to the coasts of Australia and the southern ocean. The most of the species of *Sporochnus*, which like *Bellotia* are among the most beautiful of olive-brown Algæ, are Australian; *Bellotia*, *Encyothalia*, and *Perithalia* inhabit the same region. *Sporochnus*, *Nereia*, and *Carpomitra* enter the warm Atlantic, and one species of *Sporochnus* (*S. pedunculatus*) and *Carpomitra Cabrerœ* occur in British seas.

Two puzzling types, viz. *Spermatochnus* and *Stilophora* (with *Halorhiza*) may be conveniently dealt with here as supplementary to the *Sporochnaceæ*. Their diversity consists in their vegetative structure and development, which appear to be intermediate between this order and *Chordariaceæ*, as are also their reproductive characters. The difficulty of placing them has been solved by making separate orders, viz. *Spermatochnaceæ* and *Stilophoraceæ*, for their reception, but considering how much remains to be discovered in the neighbouring groups, it appears to be scarcely justifiable to add, on grounds mainly of vegetative development, to the already excessive number of orders in the *Phœophyceæ*.

Spermatochnus, which occurs in British seas and on the Scandinavian shores of the North Sea, has been minutely studied by Reinke. It has a filiform thallus, consisting of primarily a single central row of cells, surrounded by a mantle of parenchymatous cells. It grows by the division of an apical cell, and

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the enveloping mantle of filaments is given off in whorls and surrounds the central axial strand. This mantle, ultimately several cells thick, takes on a

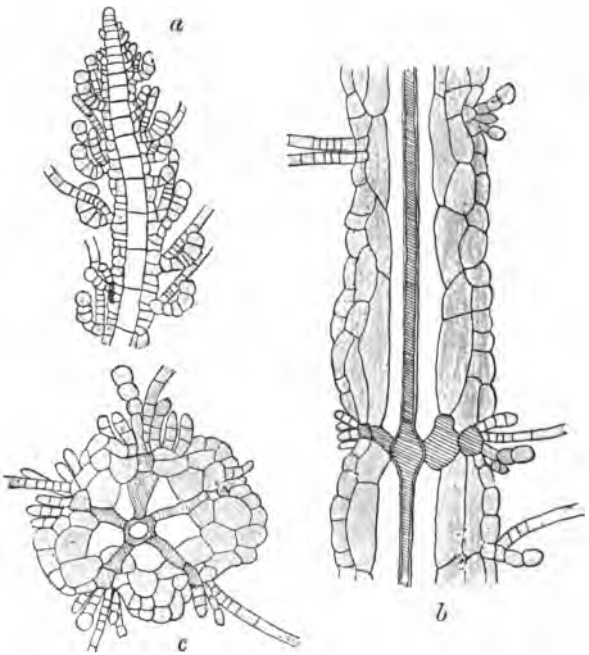


FIG. 19.—*Spermatochnus paradoxus.* *a*, longitudinal section of a young stem; *b*, ditto of a mature stem; *c*, section through a node. Highly magnified. (After Reinke.)

parenchymatous form and gradually becomes detached from the axial row, except at the insertions of the whorls, and an intercellular space intervenes from whorl to whorl between the axial row and the mantle.

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The sori of unilocular sporangia are produced opposite the whorls, and the obovate sporangia arise as lateral outgrowths of filaments produced by the superficial cells.

Stilophora (of which *S. rhizodes* is British, North Atlantic, and Mediterranean, and *S. tuberculosa*, like *Halorhiza*, Baltic) has a filiform thallus with axial strands of cells which grow in length by division of the cells immediately below the apex, and a mantle of tissue enveloping this central axial tissue. The mantle consists of a few layers of parenchymatous cells, and originates in the branches of the axial series below the growing-point. The cells of the mantle diminish in size towards the exterior. Ultimately, through the separation of the axial tissue, the interior of the thallus becomes hollow. It differs further from the above forms and approaches the *Chordariaceæ* in having both unilocular (obovate) and plurilocular sporangia, the latter with the loculi in one row. Both unilocular and plurilocular sporangia arise as lateral outgrowths of hairs produced by the superficial cells.



FIG. 20 — *Stilophora rhizodes*. Longitudinal section of growing point. Highly magnified. (After Reinke.)

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CHORDARIACEÆ.

General Characters.—The *Chordariaceæ* are a somewhat ill-defined assemblage of forms, agreeing in the possession of a slimy thallus, varying considerably, however, in its outward shape and mode of development, most frequently strand-like, but in some cases cushion-shaped and clothed in all cases with filaments of which the primary function is assimilative. Both plurilocular and unilocular sporangia occur, and these also vary in their mode of origin. The unilocular sporangia arise either in the place of the assimilative filaments or as lateral outgrowths of these, while the plurilocular sporangia are produced either in similar fashion or by the transformation of a portion of the assimilative filaments.

The Thallus.—Though there are gaps in our knowledge of the development of a number of the genera, it is probable that most of those having a strand-like growth more or less resemble *Chordaria* in this respect. It has an axial tissue of parenchymatous character, clothed with assimilative filaments and hairs. Growth in length is effected by the division of the subterminal cells of the thallus, which contribute to the growth of the axial tissue on the one hand and to the production of terminal assimilative filaments on the other. These eventually, by the production of new ones and the progressive growth of the thallus, are pushed aside and take the position of lateral filaments. More simple modifications of this mode of development occur in the other genera of

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similar habit of growth. Irregularly globular and half-globular, corrugated forms of thallus with hollow interior, like *Leathesia*, occur, and consist at the most of vertical or oblique cell-rows, more or less

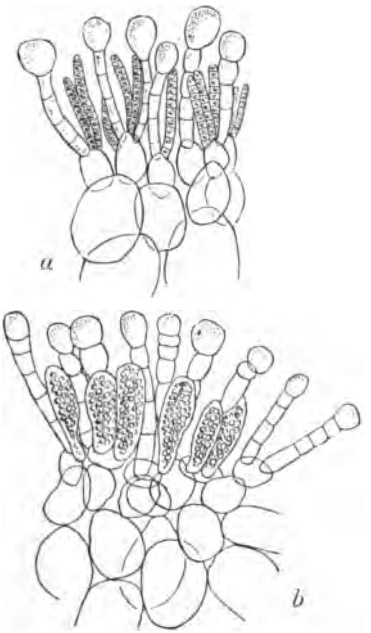


FIG. 21.—*Leathesia difformis*. *a*, plurilocular, and *b*, unilocular sporangia. Highly magnified.

branched, almost colourless within and giving rise externally to the characteristic assimilative filaments. In *Myrionema*, *Microspongium*, and allied genera, the assimilative filaments spring from a basal cushion of one or two layers of parenchymatous cells, or even of

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branching filaments (*Herponema*), and this cushion-like thallus grows by the division of the peripheral cells. The assimilative filaments arise in centrifugal order, and grow by the division of their apical cells or their upper cells.

The Reproductive Organs.—The unilocular sporangia occur mostly singly, not in sori, but fairly evenly distributed over the thallus, and either as lateral out-growths of assimilative filaments or in place of these. In *Myrionema* they spring directly from the basal cushion. They are relatively large,

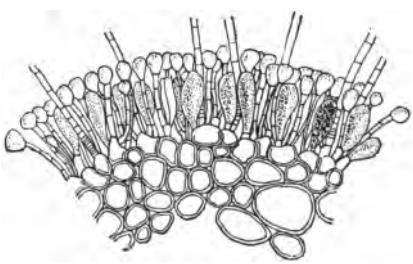


FIG. 22.—*Chordaria divaricata.* Transverse section of part of thallus, showing sporangia. Highly magnified. (After Reinke.)

and vary in form from oval, obovate, clavate, to cylindrical, with irregular lateral protuberances (*Petrospongium*). The plurilocular sporangia are of diverse origin, as stated above, and have sometimes one, sometimes several rows of loculi.

The genera composing the *Chordariaceæ* have been placed in many different orders by recent authors, and though no great degree of natural affinity can be claimed for the group as it stands, there are certain merits of simplicity in its favour, as a provisional group at all events.

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The Geographical Distribution is throughout all seas, but the majority of the forms occur in the North Atlantic. *Chordaria*, *Mesoglœa*, *Castagnea*, *Myriocladia*, *Petrospongium*, *Leathesia*, *Myriactis*, and *Myrionema* occur in British seas.

ELACHISTACEÆ

General Characters.—In its most simple form the thallus consists of a mere tuft of branching filaments with basipetal growth in length, but cushion-like forms of thallus occur, composed of a basal layer clothed with densely packed upright assimilative filaments. The unilocular sporangia, mostly ovate or pyriform in shape, arise as lateral out-growths from the assimilative filaments, while the plurilocular sporangia (giving rise to gametes, which in one case at least have been observed to conjugate) are produced either in place of such filaments or by the differentiation of a cell of one of them, or as an out-growth of such a cell. Considerable diversity occurs within the order in the development of the last-mentioned bodies.

The Thallus in no case attains a greater stature than minute, filamentous tufts or patches, and in most cases is epiphytic on larger Algæ, especially *Fucaceæ*, inhabiting in some cases even the conceptacles of these seaweeds. The rhizoids penetrate the tissues of the host-plants, and some of the forms send out runners, which traverse the tissues or creep over the surface, giving rise to new plants by this

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vegetative mode of propagation. The thallus originates in a creeping filament which sends up at frequent intervals perpendicular branches. These grow at first by division of most of their cells, but eventually a growing-point or meristematic region is localised, above which the filaments assume the character of the assimilative filaments, either remaining as simple rows of chromatophore-containing cells, or, by cell-divisions parallel to the axis of each filament, becoming polysiphonous (or consisting of tiers of cells), or even attaining a parenchymatous character. The portions of the original filaments below the meristematic region give rise to the basal tissue, the cell-rows of which branch, and the whole ultimately in some cases attains a compact character. This tissue, which remains almost colourless, bears the assimilative filaments, and among them the reproductive organs and paraphyses. The assimilative filaments are frequently shed, exposing the reproductive organs, and in one case at least this shedding of the filaments precedes the development of the plurilocular sporangia. Kjellman thinks it possible that there may be perennial forms which periodically shed the assimilative filaments and renew them from persistent growing-points. In the case of the more simple free filamentous forms there is naturally no such sharp distinction of tissue.

The Reproductive Organs.—The unilocular sporangia are ovate or pyriform, and mostly arise laterally from the base of the assimilative filaments. They are generally sessile and relatively large. The plurilocular sporangia of *Elachista* are the most simple

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of all. They are long, filamentous, consisting of a single series of loculi, and originate from the base of assimilative filaments. In *Leptonema* certain of the upper cells of the filaments become the mother-cells of the plurilocular sporangia. These cells bulge out laterally and divide into 3–6 transverse loculi, each with one or two gametes. In *Halothrix* the matter is more complex. The mother-cell divides up into a considerable number of cells, of which those at the periphery grow out into rows of loculi which contain each a single gamete. *Giraudia*, of which the gametes have been observed to conjugate, possesses two sorts of plurilocular sporangia. The one kind are tapering filamentous bodies of several rows of loculi, otherwise resembling those of *Elachista* in origin. The other kind are of singular appearance, originating from the cells of the assimilative filaments by transverse and radial divisions, and forming clusters of ovate plurilocular sporangia, each of several rows of loculi. This second kind approaches the *Halothrix* type in general character.

The Geographical Distribution of the *Elachistaceæ* is general, but most of the forms are from the North Atlantic. *Elachista*, *Halothrix*, *Giraudia*, and *Leptonema* are British.

The genus *Myriotrichia* (North Atlantic), of which *M. clavæformis* is British, stands in a somewhat isolated systematic position. It has been placed with the forms ranged under *Encœliaceæ*, and in a separate position by itself as the type of an order *Myriotrichiaceæ*, while its relationship with *Elachistaceæ* is not denied. Further research, not so much

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on its characters as on those allied groups, will no doubt better assure its position here or elsewhere. Its species are epiphytic on other Algæ and show small differentiation as regards the thallus. *M.*

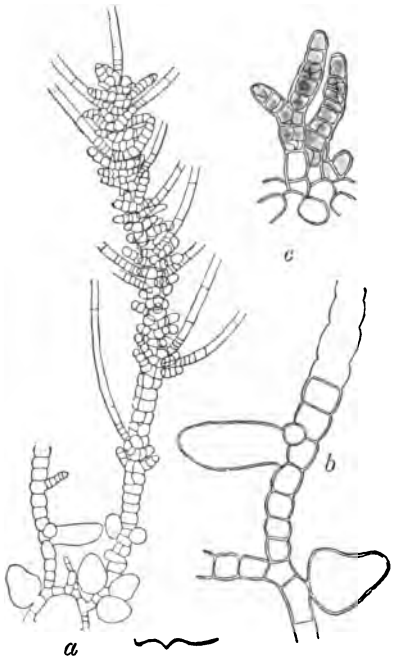


FIG. 23.—*Myriotrichia clavæformis*. *a*, plant with sporangia, magnified ; *b*, part of same, more highly magnified ; *c*, plurilocular sporangia. (After N. Karsakoff.)

clavæformis, which grows on *Scytosiphon*, is a small filamentous Alga, densely clothed with branches and hairs above, while remaining simple below. It consists at first of a cell-row, growing in length by

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intercalary transverse divisions. Then follow vertical divisions in greater or less number until the axis, which terminates upwards in a hair, commonly consists of tiers of four or more cells. At the base, at least while transverse division continues, the axis remains composed of a single row of cells. The external cells of the upper portion produce short processes which bear cell-rows or sporangia. These branches terminate in hairs, and frequently bear farther branches similarly tipped, which in turn bear reproductive organs or more rarely branches again. The unilocular sporangia are globular or slightly ovate, with a small wart at the apex, and occur singly or in whorls on the axis and branches, being morphologically the equivalent of branches. The plurilocular sporangia are cylindrical and usually of one row of loculi, and are borne singly and in tufts on the short processes of the axis. There are differences of size among them, and this difference indicates a farther one—viz., in the nature of the contents. The small sporangia give rise generally to four large gametes, the others six to twelve (commonly eight) gametes. Conjugation takes place only between a large gamete and a small one, and apparently both when they are in a state of mobility and also at the moment of coming to rest. The point of contact is the hyaline part when they are in a semi-mobile state, but when fully mobile there is no general rule in this respect. The large one appears to absorb the small one, and after one to two hours, nothing but the two pigment spots remain to indicate their previous separate existence.

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DICTYOSIPHONACEÆ.

General Characters.—This group is not well defined, but will possibly gain in this respect from future investigation. The thallus is of medium stature, of two layers of parenchymatous tissue, and grows in length by an apical cell. Only unilocular sporangia are known.

The Thallus is attached to its substratum by a dense weft of root-hairs, and consists of a loosely connected internal tissue of elongated cells, attached to each other, mostly by lateral processes, and diminishing in length towards the outside, where this tissue merges into the cortical layer. It eventually becomes hollow in nearly all cases. The outer cortical layer of *Dictyosiphon* is parenchymatous, and in *Gobia* consists of a somewhat loosely compacted series of cell-rows running outwards. In *Dictyosiphon*, irregular branching is fairly copious, in *Gobia* there is sometimes no branching at all, and if present it is always spare and irregular. *Scytothamnus*, about the development of which comparatively little is known, is repeatedly branched. Hairs are produced abundantly from the cortical cells, especially on young plants.

The Reproductive Organs are represented, so far as is known, only by unilocular sporangia, which arise as the equivalents of cortical cells. The observations of Areschoug suggest that the zoospores produced in these may occasionally, at least, play the part of gametes, but the matter requires confirmation. So far as our knowledge of the group goes, it is plain

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that no sure indication of its relationship is thus afforded.

The Geographical Distribution is in north and south temperate seas, extending to the Arctic at least. *Dictyosiphon* occurs in both the North Atlantic and southern ocean (*D. fœniculaceus, D. hippuroides, D. Chordaria,* and *D. Mesoglœa* being British), *Gobia* in the Baltic, and *Scytothamnus* in the southern ocean exclusively.

DESMARESTIACEÆ

General Characters.—The thallus consists of a primary branching row of cells with a growing point below the apex; beneath this growing point a mantle of tissue is produced which clothes the primary cell-row and eventually forms a thallus of considerable thickness. Its growth in length is maintained by the subterminal growing point above this secondary mantle of tissue. Unilocular sporangia are formed (*Desmarestia*) by the differentiation of superficial cells below the growing point; and plurilocular sporangia (*Arthrocladia*) from rows of cells.

The Thallus is usually of considerable stature, especially in the species of *Desmarestia.* Two sorts of branches are formed—long ones, and, more abundantly, short ones. They are generally in two rows and mostly alternate, but sometimes opposite. The primary row of cells forming the thallus produces branches abundantly, and these as well as the main axis grow in length by the repeated transverse

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divisions of the cells of the growing point beneath the apex. The characteristic mantle which forms the secondary growth in thickness originates from the basal cells of the lateral branches arising directly below the growing point; the cell-filaments so produced unite in parenchymatous fashion, and remain closely adherent to the primary row and divide in

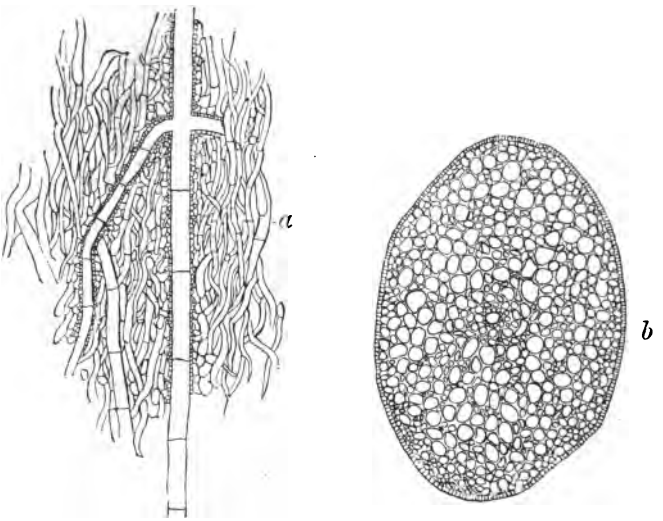


FIG. 24.—*Desmarestia aculeata*. *a*, longitudinal section showing mantle of filaments; *b*, transverse section. Highly magnified.

several directions. The mantle ultimately consists of two layers of tissue—viz., a cortical layer consisting of small cells engaged in assimilation, and an inner layer of larger cells diminishing in size towards the outside. In some cases these larger cells have smaller ones intermixed with them. In the forma-

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tion of the long branches the activity of the growing point is mainly directed to the development of the branches below the growing point, while during the formation of the short ones, most of the cells produced reinforce the growth in length of the terminal shoot.

The Reproductive Organs.—Unilocular sporangia are known in *Desmarestia viridis*, and are the equivalents of superficial cells. In *Arthrocladia* club-shaped chains of cells arising above the growing-point of the short branches form the plurilocular sporangia. Farther information is greatly needed on the subject of the reproductive organs of this group, and observations on the species of *Desmarestia* in particular.

The Geographical Distribution is mainly in the north and south temperate seas. *Arthrocladia villosa*, and *Desmarestia viridis*, *D. aculeata*, *D. ligulata*, *D. Dudresnayi* are British, but most species of the latter genus belong to the southern ocean.

STRIARIACEÆ.

General Characters.—The thallus, which attains considerable length in many of the forms, is of parenchymatous structure, and variously branched. It grows in length at a meristematic region below the apex. Both unilocular and plurilocular sporangia occur, developed as equivalents of superficial cells or as outgrowths of such.

The Thallus, which is rarely simple, but in most

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cases copiously branched and clothed with hairs (including a terminal one), shows slight differentiation of tissues. In the more simple forms an articulated appearance is presented, the upper portions, particularly of the branches, remaining as rows of single cells, while the lower portions consist of equal tiers of cells produced by division lengthwise of the original single row. In the more highly differentiated forms this appearance of articulation is lost, since the thallus consists of two tissue layers, a cortical layer of short rectangular cells, and an interior tissue of elongated cells, also rectangular in shape in most cases. In *Striaria*, however, the cells of the interior tissue are roundish in cross-section, and they line a hollow interior in the fully developed plants. The growth in length is by a subterminal intercalary growing point, but in *Kjellmania* the cells of the whole thallus participate in this process. In *Phlœospora*, portions of the shoot are detached and lead to vegetative propagation.

The Reproductive Organs.—Both unilocular and plurilocular sporangia are, as a rule, the equivalents of superficial cells, and are generally partially immersed in the tissue. They occur in some cases singly, but more frequently in sori or patches covering wholly or in part zones of the thallus. In *Striaria* paraphyses are produced among the sporangia. *Kjellmania sorifera* presents a somewhat aberrant type. Its peculiarity of growth has been mentioned above, and in point of reproduction it presents the further singularity of possessing (like *Giraudia*) two kinds of plurilocular sporangia. The one kind are simply

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interstitial cells of the thallus which divide up transversely and longitudinally to form plurilocular sporangia. These occur generally in numbers adjacent to each other. The other kind, which appear to be more common, arise by a process from a superficial cell (or one of the cells where the thallus consists of a single row). This process divides

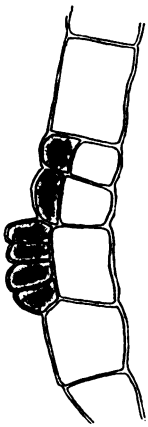


FIG. 25.— *Kjellmania sorifera*. Filament with young sorus sporangia. Highly magnified. (After Reinke)

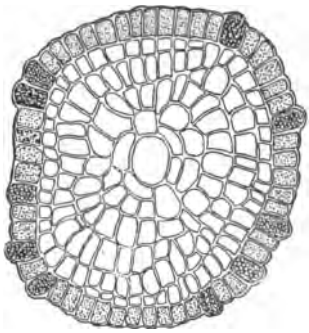


FIG. 26. — *Stictyosiphon Decaisneti*. Transverse section of thallus showing sporangia. Highly magnified.

up by walls running transversely to the axis of the plant into a sorus of cells, each of which acquires an arched apex and divides farther into 2-4 loculi one above the other. Each loculus produces a single zoospore. The whole sorus is thus in this case the product of a single superficial cell. The occurrence here and in *Giraudia* of two kinds of

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plurilocular sporangia leads to a certain amount of hesitation in adopting the presumption that these always contain gametes or even potential gametes. It recalls the difficulty presented by the case of *Ectocarpus secundus*, which possesses plurilocular sporangia and antheridia (*see p.* 68). *Zosterocarpus*, a genus recently founded by M. Bornet, appears to be most nearly related to *Kjellmania*, especially in the mode of formation of the sori of sporangia.

The Geographical Distribution is mainly in the North Atlantic and Arctic oceans. *Stictyosiphon* occurs in the Mediterranean and South Atlantic, *Kjellmania* in the Baltic, *Striaria* in the North Atlantic and Mediterranean, and *Phlœospora* in the Arctic and North Atlantic. *Striaria* and *Phlœospora* are British. Some authors regard species of *Phlœospora*, probably correctly, as belonging to *Stictyosiphon* (*e.g. Phlœospora tortilis*), which accounts for the presence of that name in British marine floras, while others restrict *Stictyosiphon* to the single species *S. adriaticus*.

Encœliaceæ.

General Characters.—Though none of the *Encœliaceæ* attain great size, the order is remarkable for the great diversity of the forms assumed by the thallus, including frond-like, filamentous, club-shaped, globular, hollow, reticulate, &c. shapes, though they agree in none of them having a definite system of branching. They are of parenchymatous structure and

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possess no definite growing point. The reproductive organs are both unilocular and plurilocular sporangia arising by the differentiation of a superficial cell or of an outgrowth from one. The conjugation of gametes has been observed in one form.

The Thallus in the filamentous form is articulated, and consists of several rows of cells, but sometimes partially or even wholly of a single row. However, most of the forms exhibit both a cortical tissue and an internal one. The internal tissue consists of large parenchymatous cells, and the cortical layer of smaller assimilative cells, though these are commonly of relatively greater size than in allied groups. Hairs and paraphyses sometimes spring from the superficial cells, the hairs with basal growth (at least in the case of *Punctaria*, and more notably *Hydroclathrus*) from pits resembling cryptostomata of simple structure. The attachment of the thallus to the substratum is either by means of a disc or by a weft of rhizoids. Immediately above the attachment the base of the thallus is commonly attenuated to a thin, solid and short stalk. There is no true growing point, and the growth is distributed more or less equally over the whole thallus, but persists at the base, as a rule, for a time after it has ceased elsewhere. The development of the cryptostomata has been observed in *Hydroclathrus*. In a surface view "an isolated cell or several cells in a group become separated off from the surrounding epidermis, each loses its polygonal shape and becomes cylindrical. . . . In a radial section of such a group each cell is seen to be divided by a transverse wall, but there is no indication of

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such longitudinal division as occurs in neighbouring epidermal cells. The lower of the two cells again

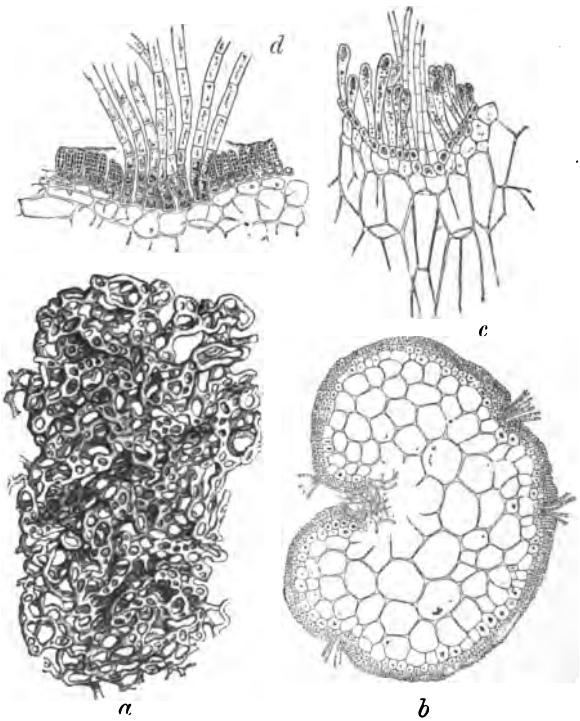


FIG. 27.—*a*, *Hydroclathrus cancellatus* one-half natural size ; *b*, section of thallus ; *c*, *H. sinuosus*, cryptostoma and paraphyses ; *d*, mature cryptostoma with young sporangia. *b*, *c*, *d* highly magnified. (After M. O. Mitchell, in *Phyc. Mem.*)

divides transversely, and this method of division continues till a long row of cells has been formed, making in fact a hair. Simultaneously with the

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formation of these hairs, the cells immediately surrounding them undergo similar changes, and thus the cryptostoma enlarges radially. Meanwhile the thallus continues its growth, so that the basal cells of the hairs which were originally in the same plane as the epidermis have now come to lie below it, and the whole structure is suggestive of a conceptacle."[1] It is interesting to note that the formation of a cryptostoma is the starting point for the formation of a sorus of plurilocular sporangia from the adjacent epidermal cells. This spreads radially from the cryptostoma as from a centre, and the formation of sporangia is succeeded, after these have disappeared, by that of club-shaped paraphyses from the basal cells that bore the sporangia. While the basal cells nearest the cryptostoma are producing paraphyses, those farthest away are still giving rise to sporangia. Gradually the paraphyses replace the sporangia until the latter disappear, and there is left a group of paraphyses with a central cryptostoma. This occurrence of a central cryptostoma in the sorus recalls the case of *Adenocystis*[2] (*Laminariaceæ*, p. 84), though it presents a contrast with the conceptacle of *Splachnidium*, which bears hairs only at first, and sporangia later on. Though not comparable with the more highly developed cryptostomata of the *Fucaceæ*, we have here an elementary form of cryptostoma, and it is instructive to observe that the development of cryptostoma and sorus originates in the alteration of

[1] M. O. Mitchell, in Murray's *Phycological Memoirs*, part ii., p. 54.
[2] Murray in *Phyc. Mem.*, part ii., p. 62.

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form and division of one initial cell (or at most a small group) derived from the epidermal layer.

The Reproductive Organs, both unilocular and plurilocular, are either differentiated superficial or epidermal cells or outgrowths of these. They are accompanied or succeeded, as has been noted above, by the formation of paraphyses. While in such genera as *Desmotrichum*, *Punctaria*, &c., the epidermal cells in question undergo but little differentiation, in *Scytosiphon*, *Hydroclathrus*, and other genera, the cells giving rise to plurilocular sporangia undergo considerable elongation and division in the process. The globular unilocular sporangia of *Asperococcus*, standing free from the surface of the plant among paraphyses, originate in outgrowths from the epidermal layer—as the paraphyses do.

The order is formed of three others recognised formerly as *Punctariaceæ*, *Scytosiphonaceæ*, and *Asperococcaceæ*, together with the genera *Coilodesme* and *Myelophycus*—a grouping of them justified by Kjellman (Engler and Prantl's *Nat. Pflanzenfamilien*, part i., p. 197).

The Geographical Distribution is fairly even throughout all seas, but more abundant in temperate waters. *Desmotrichum*, *Punctaria*, *Litosiphon*, *Scytosiphon*, *Phyllitis*, and *Asperococcus* occur in British seas.

Ralfsiaceæ.

General Characters.—This small order embraces plants of a very undifferentiated vegetative structure and of a crust-like habit. The reproductive organs

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are of two kinds, plurilocular (containing presumptive gametes) and unilocular.

The Thallus of *Ralfsia* forms leathery crusts on rocks, &c., and though at first almost circular, becomes ultimately of irregular outline. It attains considerable thickness in the more central portion, and decreases towards the margin. The cells, each with one chromatophore, are in vertical series and form a parenchymatous tissue; those of the margin effecting by division the extension of the thallus, while the superficial cells similarly add to its thickness. It is attached to the substratum either directly or by means of root-hairs. On the upper surface there occur single hairs, or in other cases tufts, sometimes springing from pits which, however, do not appear to exhibit a special development like the cryptostomata of other orders. By a process of overlapping of new crusts on older ones, the thickness of the thallus is often considerably increased. In *Lithoderma* there is no notable difference from *Ralfsia* in the development and structure of the thallus.

The Reproductive Organs.—Until recently only unilocular sporangia were known in the case of *Ralfsia*. They are obovate and arise as lateral processes from septate hairs, which are in turn direct prolongations of the superficial cells of the thallus. Though of lateral origin, the sporangia assume a terminal position by pushing aside the true terminal shoot. The plurilocular sporangia, recently discovered by Mr. Batters, are of similar origin, but with them are no paraphyses. The hairs or paraphyses grow mainly, if not wholly,

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by the division of their apical cells, and, at the margin of a sorus, where they may be seen in an early stage of development, push off and cause to exfoliate the original cuticuloid gelatinous layer of the epidermis. In *Lithoderma* sporangia of both kinds occur in sori, but on different plants. The plurilocular bodies, which may be presumed to give rise to gametes, occur as lateral off-shoots from special branches arising in turn from superficial cells. These gametangia are either a single row of cells, or more frequently several rows, and are more or less cylindrical in shape. The unilocular sporangia are terminal bodies—in fact transformed superficial cells, and are mostly obovate. The actual life-history has not been followed, but the relationship with *Ralfsia* cannot be doubted. The general relationships of the order are vague, but probably *Chordariaceæ* of which *Ralfsiaceæ* may be degenerate allies, and *Ectocarpaceæ* (especially *Ascocyclus*) exhibit the most distinct claims.

The Geographical Distribution extends from the polar seas to the tropics, and though the species are always few, the maximum is attained in the North Atlantic. The distribution of the six or seven species of *Lithoderma* is of limited range so far as is at present known. They occur, however, both in fresh-water and in the sea. The marine forms are found in the Arctic Sea, North Atlantic, and Mediterranean, while the two fresh-water forms occur in the south of France, Germany, and Sweden. *L. fatiscens* has recently been discovered on the British coasts.

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SPHACELARIACEÆ.

General Characters.—The thallus consists of erect shoots springing from a more or less extensive basal creeping cushion fixed to the substratum. The erect shoots are more or less branched and may be as in the most reduced case a simple cell-row, or an articulated filament consisting below of tiers of cells of equal height, or the latter case may be further developed by the addition of a cortical tissue. Growth in length is effected by an apical cell. The reproductive organs are both unilocular and plurilocular and are borne on short branches. Vegetative propagation by gemmæ occurs.

The Thallus.—The most simple form is to be found in the exceptional case of *Battersia mirabilis*, for the inclusion of which the definition of the order has to be somewhat stretched, since this plant exhibits in many respects a striking resemblance to *Lithoderma*, and in these same points a divergence from *Sphacelariaceæ*. The thallus of *Battersia* consists of a creeping cushion of several layers of cells fixed to the substratum by its undersurface, and giving off upwards short simple or branching shoots which bear the sporangia terminally. These shoots consist of single cell-rows, though occasionally they form several rows at the base, after longitudinal division of the cells.

Most of the *Sphacelariaceæ* spring from a basal cushion which grows by its marginal cells, or from a weft of rhizoids which penetrate the tissue of the

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host on which they may be epiphytic. Runners proceed from these, which sometimes give rise to new plants. The erect shoots are mostly articulated

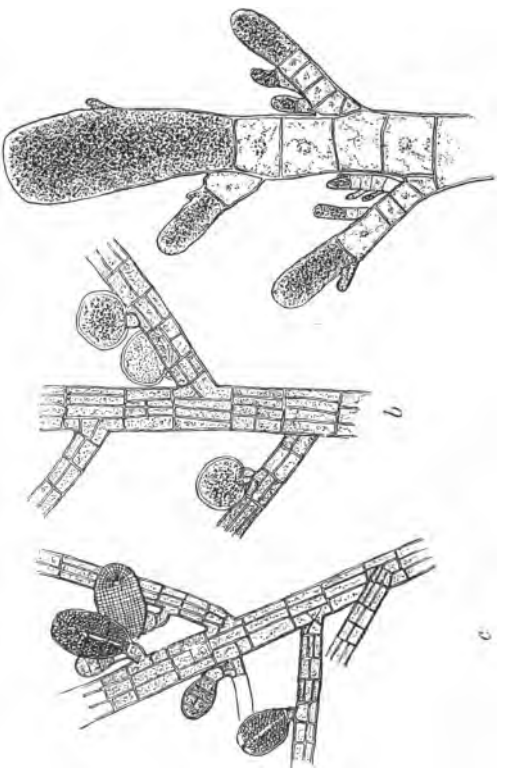


FIG. 28.—*a*, *Sphacelaria filicina*, tip of filament; *b*, *S. cirrhosa*, showing unilocular sporangia; *c*, the same showing plurilocular sporangia. Highly magnified.

filaments consisting of tiers of cells and terminating upwards in an apical cell, by division of which growth takes place. This apical cell is of relatively large size and the shoot possesses the remarkable power

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of being able to renew the apical cell after the original one has perished. This property is akin to another exhibited by the branches which bear the gemmæ and sporangia. After the fall of a gemma, the remaining basal cells of the branch that bore it may proceed to grow and form another one. Similarly after the emptying of a sporangium, the branch may grow through the membrane and form a new sporangium.

The branches are either all of equal morphological value or there may be a distinction between long and short ones. The latter are alternate in *Stypocaulon* and *Halopteris*, opposite in *Chætopteris*, and in whorls in *Cladostephus*. They are either themselves unbranched (*Stypocaulon* and *Chætopteris*), or branched on one side (*Cladostephus*), or they resemble in miniature the branching of the long branches (*Halopteris*). In *Stypocaulon*, *Cladostephus*, and not so markedly in *Halopteris*, the outermost cells of the filaments of the thallus undergo farther division and produce a cortical tissue of small cells which obscures the articulation of the original thallus. In *Sphacelaria* and *Chætopteris* this articulation of tiers of cells remains apparent throughout the life of the plants. A farther modification takes place in *Cladostephus*, *Stypocaulon*, *Halopteris*, and some species of *Sphacelaria* by the outgrowth of rhizoid filaments from the older parts of the shoots. These filaments grow downwards, creeping over the thallus, and form a kind of mantle over the lower parts of the shoots.

Some of the *Sphacelariaceæ* are subject to the

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attack of parasitic entophytal *Chytridiaceæ*, and thus present appearances which have been a source of error in their interpretation.

The Reproductive Organs are both unilocular and plurilocular sporangia, and the different kinds occur as a rule on different plants. They are rarely (as in *Battersia*) differentiated terminal cells of the axis or ordinary branches, but generally the terminal cells of special branches (their stalks, in fact), which arise sometimes singly, sometimes in tufts, in a considerable variety of relations to the axis and branches in the different genera. The unilocular sporangia are mostly round or oval in form, the plurilocular cylindrical or obovate. The latter in some instances may be branched at the base.

The gemmæ, which, so far as is known, are characteristic of this and the following order only among *Phæophyceæ*, are short branches, which cease to grow in length and send out two or three lateral short processes at the top, while the apical cell which had ceased to grow in length, emits a hair. The basal cell remains undivided and the gemma breaks off above it. On being set free, the terminal cells of the short processes or of the stalk grow out into a creeping filament, which bears new shoots as lateral branches.

The Geographical Distribution is a general one, but possesses most representatives in north and south temperate seas, especially on the coasts of the North Atlantic and the Australian region. *Battersia* (peculiar to Britain), *Sphacelaria*, *Chætopteris*, *Cladostephus*, *Halopteris*, and *Stypocaulon* are represented

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on the British coasts; *Sphacella* in the Mediterranean; *Phloiocaulon*, *Anisocladus*, and *Ptilopogon* in the Southern Ocean. *Sphacelaria* is represented in all seas.

CHORISTOCARPACEÆ.

General Characters.—The thallus is filamentous, consisting of a single row of cells, and possesses an apical cell by which it grows in length. The reproductive organs, both unilocular and plurilocular sporangia, arise as lateral outgrowths of the filaments, as do also the vegetative gemmæ.

The Thallus is in all cases filamentous and branched—never of more than one cell-row. The apical cell produces all the cells—*i.e.*, there is no intercalary growth whatever.

The Reproductive Organs.—The plurilocular sporangia of *Discosporangium* form a remarkable rectangular plate one layer thick, arising laterally from a slight outward bulging of the wall of one of the cells of the thallus. The loculi open outwards. In *Choristocarpus* the corresponding bodies more nearly approach those of *Ectocarpaceæ*. In *Pleurocladia* (a fresh-water form placed here) the plurilocular sporangia also resemble those of *Ectocarpaceæ*, and this genus further possesses unilocular sporangia (not known in *Discosporangium* and *Choristocarpus*) of similar type.

The gemmæ are known only in *Choristocarpus* and are lateral outgrowths of two, rarely three, cells, the upper being the larger. After they are shed the

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stalk-cell may proceed to form another, as in *Sphacelariaceæ*. In vegetative propagation and in the growth of the thallus—viz., the absence of intercalary growth in length—the *Choristocarpaceæ* appear to be related to the *Sphacelariaceæ*, while the type of reproductive organs points more to the *Ectocarpaceæ*.

The Geographical Distribution of this small order, consisting of the three genera named (*Pleurocladia*, with two species, the others with one each) is very limited. *Pleurocladia* is purely fresh-water, one species occurring near Berlin, the other in Kerguelen Land, while the other genera are both marine and confined to the Mediterranean.

ECTOCARPACEÆ.

General Characters.—The thallus of the *Ectocarpaceæ* is always of simple character and commonly consists of erect, simple or branched filaments springing from a creeping filament or flat layer, or it may be reduced to a creeping filament or layer, from which the reproductive organs spring. These are both unilocular and plurilocular sporangia.

The Thallus.—The primary creeping filament grows by division of the terminal cell or cells and bears in the most simple cases (*e.g.*, *Streblonema*) only reproductive organs and hyaline hairs with basal growth, or tufts of erect filaments (*e.g.*, *Ectocarpus*), which grow by intercalary divisions without a definitely localised growing-point. These divisions are at first fairly general throughout the filament;

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they cease first at the apex, which becomes hyaline and elongate, and eventually continue only in places here and there. The filaments, simple or branched, are for the most part of one single cell-row and rarely divided by longitudinal walls. Sometimes the cells of the erect filaments produce rhizoids which descending form a loose weft about the shoot. Where a basal horizontal layer occurs (*e.g.*, *Ascocyclus* and *Phycocelis*) it grows by peripheral cell-divisions and bears on its upper surface sporangia, hairs and paraphyses.

The Reproductive Organs.—The plurilocular sporangia, which may be of one or more rows of loculi, are formed either by the differentiation of the upper portion of a branch or an intercalary part of it; or they are definite outgrowths of cells of the erect filaments or primary basal layer. In *Sorocarpus* they occur in dense clusters; but in the other genera they are free like the branches and mostly elongate, cylindrical, or oval in shape. They are commonly of several rows of loculi, but sometimes of a single row, wholly or in part. The gametes escape from all the loculi usually by an apical or lateral opening, and their conjugation is of a peculiar character. In *Ectocarpus siliculosus*, in which it has been carefully observed, the ♀ gamete first comes to rest and is then surrounded by numerous ♂ gametes, one of which succeeds in conjugating with the ♀ gamete. That the ♀ gamete should first come to rest before becoming susceptible of conjugation recalls the case of *Cutleria*, and also in part that of *Myriotrichia*. The occurrence of bodies which can only be termed antheridia in

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Ectocarpus secundus and *E. Lebelii*, besides ordinary plurilocular sporangia, has already been mentioned, and their full significance can be little more than guessed until much more is known of



FIG. 29.—*Ectocarpus confervoides*. Filament with unilocular sporangia, and one plurilocular sporangium. Highly magnified.

the reproductive processes in *Phæophyceæ*. Meantime, observation of the possible relation of their antherozoids, which fully resemble those of *Fucaceæ*, *Cutleriaceæ* and *Tilopteridaceæ*, with the gametes of the plurilocular sporangia, may help the matter.

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The unilocular sporangia occur (*Pylaiella*) in rows of intercalary cells or (*Isthmoplea, Ectocarpus*, &c.) as lateral outgrowths of the cells, generally sessile, and oval or globular in form.

The relationship of the order is undoubtedly a close one with *Sphacelariaceæ* and other orders here placed near it, but facts briefly alluded to above compel one to look to orders like *Tilopteridaceæ* for other marks of near alliance.

The Geographical Distribution of this large order is fairly general, but is most markedly abundant in the North Atlantic—though this probably means no more than that it has been most studied here. *Streblonema, Ectocarpus* (many species), *Isthmoplea, Pylaiella, Sorocarpus, Ascocyclus* occur in British seas.

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SUB-CLASS II

CHLOROPHYCEÆ

THE *Chlorophyceæ* attain their finest development in fresh waters, but representatives of most of the orders occur in the sea. The multicellular forms never attain a higher stage of development than branched or simple cell-rows or flat expanses of indefinite form. The unicellular forms, however, in addition to the simple Algæ usually so called, are represented by the multinucleate orders in which the highly developed thallus is a conspicuous feature.

Oogamous reproduction occurs here, as in the *Phæophyceæ*, but mostly in fresh-water forms. It is represented in the sea in the marine species of *Vaucheria* only, and this type of oogamous reproduction differs from that of *Phæophyceæ* (*Fucaceæ*) in respect of the fact that the fertilised oosphere is not extruded but remains *in sitû* in the parent plant. The fact of the occurrence of this high type of reproduction almost exclusively in fresh-water forms, and in those Algæ with chromatophores most nearly resembling terrestrial vegetation, points to this group

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PLATE III.

1. CODIUM TOMENTOSUM.

2. CODIUM BURSA.

3. HALICYSTIS OVALIS.

4. BRYOPSIS PLUMOSA.

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as most probably nearer the lower limits of archegoniate plants than are any other Algæ.

The other *Chlorophyceæ* exhibit isogamous reproduction—viz., the conjugation of equal gametes provided with cilia; and in the case of the Conjugatæ, which are confined to fresh-water, the conjugation of non-motile gametes.

Non-sexual reproduction by zoospores and unciliated spores also occurs freely and abundantly in the *Chlorophyceæ*.

The *Caulerpaceæ*, *Vaucheriaceæ*, *Codiaceæ*, *Udoteaceæ*, *Dasycladaceæ*, and *Valoniaceæ* which form a group together (usually called *Siphoneæ*) are distinguished from all other Algæ by the fact that their often complicated thallus consists in reality of a single cell with many nuclei. In *Valonia* this one cell retains a primitive, more or less globular, shape, but in the other orders it is much branched and the branches gain coherence from being interwoven, laced together by haptera, incrustation, etc. In *Caulerpa* alone the lumen of the great cell is strengthened internally by numerous trabeculæ or crossbeams that run from wall to wall.

CAULERPACEÆ.

General Characters.—The order is represented by the single genus *Caulerpa* (though systematists have proposed to split it up into several genera on wholly insufficient grounds) containing about eighty much varied species. They are exclusively marine. In some

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respects *Caulerpa* is the most singular type in the vegetable kingdom, since it attains a variety of habit rarely to be found within the limits of a very large order, though the plants are invariably composed of the branchings of a single cell. This cell obtains



FIG. 30.—*Caulerpa phyllaphlaston* one-half natural size. (Ex. *Phyc. Mem.*)

the mechanical support, elsewhere given by cross-walls, from a system of trabeculæ or narrow beams, branching and traversing the cell from wall to wall in all directions. No reproductive organs are known, and the only method of propagation that has been discovered is by the separation of proliferous shoots.

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The Thallus.—There is hardly any type of habit assumed by the higher terrestrial plants that does not find itself represented in this singular genus. There are species named from their resemblance to mosses, club-mosses, cacti, yews, etc., etc., while others are of extremely simple form. This differentiation is not confined to the green assimilating shoot, but extends to the root-system with its creeping rhizome-like extensions. The plants frequently attain considerable stature, and are in most cases of remarkable beauty. It has been said [1] that "Nature appears to have executed in the forms of this genus a *tour de force* in exhibiting the possibilities of the siphoneous thallus — in showing that it is possible for a unicellular organism to display the varied beauties of outward form characteristic of highly-organised types; to attain by means of a lattice-work of crossbeams within the cell-body that mechanical support effected by transverse septa and separate, differentiated cellular structures for other Algæ and for the higher plants."



FIG. 31.—*Caulerpa cactoides var. gracilis* one-third natural size.

[1] *Trans. Linn. Soc. Bot.*, 2 ser., vol. iii., part 4., p. 207.

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The erect, green, assimilating shoots are, as has been indicated, very variously branched, and the species are classified mainly on the characters so displayed. They root in fine sand or mud, and commonly possess a creeping *surculus* or rhizome which gives off roots below and erect foliar shoots at intervals after the fashion of higher plants. The network of trabeculæ or cross-beams is very dense in most species, and traverses the cell-contents in all directions. They spring from the substance of the outer wall-membrane (Fig. 32, *c* and *d*), and their principal function appears to be that of imparting support to the walls, though other functions have been speculatively ascribed to them without much show of reason.

Dr. Correns has recently made a minute study[1] of the membrane, and has found that after treatment with sulphuric acid it has exhibited the formation of numerous sphærocrystals, showing differences from those of cellulose demonstrated by Gilson and Bütschli. From the tests he has imposed, he has come to the conclusion that the membrane of *Caulerpa* does not consist of cellulose in the narrow sense, but of a substance not yet fully known, and different from callus, fungus-cellulose, reserve-cellulose, etc. He has obtained similar results from two species of *Bryopsis*, and is inclined from this to regard with favour the view, otherwise vaguely indicated, of a relationship of this singular genus with *Bryopsis*.

So little indication is there, however, of relationship with other Algæ, that we have but the one fact

[1] *Ber. Deutsch. Bot. Gesellsch.*, 1894, bd. xii., p. 355.

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of its multinucleate character to guide us in assigning it a position here. The numerous species have been carefully examined without the discovery

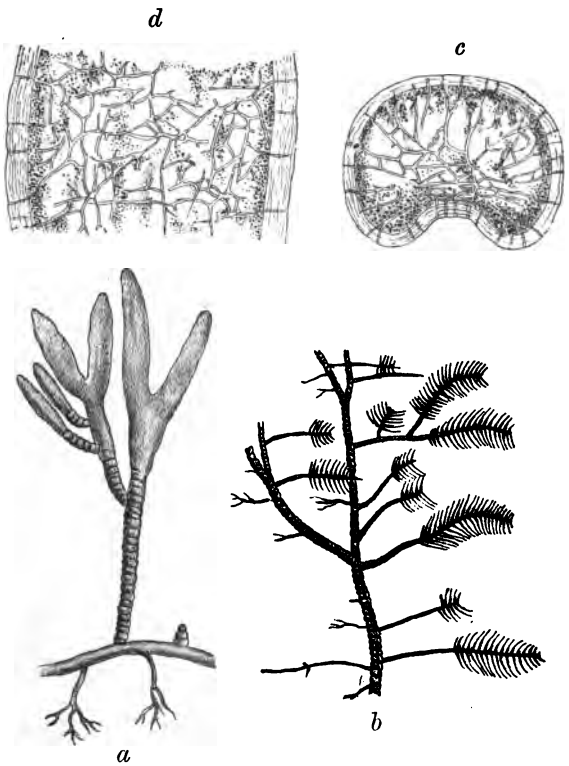


FIG. 32.—*a*, *Caulerpa ligulata* natural size; *b*, *C. Holmesiana* natural size; *c*, transverse, and *d*, longitudinal section of stem, highly magnified.

of any reproductive organs, which alone could show us its true position among the siphoneous Algæ.

By an error there has been described a genus

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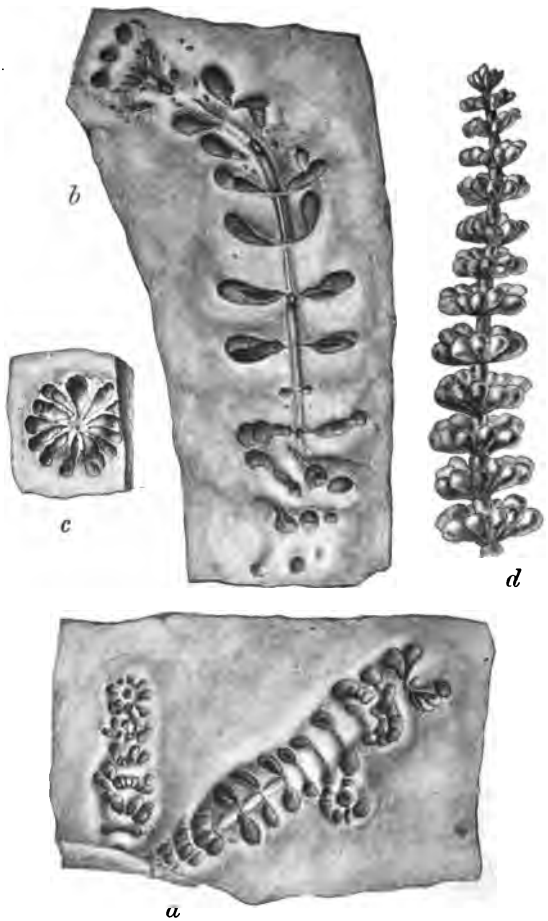


FIG. 33.—*a* and *b*, *Caulerpa Carruthersii*. *c*, section; *d*, ideal figure of same half natural size. (EX. *Phyc. Mem.*)

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Chlorodictyon, said to be related to *Caulerpa*, and its description and figure have found a place in several important books of reference. It is however not even an Alga, but a lichen without the least structural resemblance to *Caulerpa*.

The Geographical Distribution of the genus is throughout tropical and sub-tropical seas. There is one species (*C. prolifera*) in the Mediterranean, and several as far south as the Cape of Good Hope.

The name *Caulerpites* has been given to a large number of fossil remains without, in a single instance, any reason other than a more or less vague resemblance of outward form. Since the genus itself resembles so many other types, this has been almost an inevitable error on the part of those palæophytologists who choose to be content with mere impressions. A fossil *Caulerpa* (Fig. 33) from the oolite (Kimmeridge Clay), of which we possess casts in the round, stands on a firmer basis, since it not only exhibits resemblance of form, but occurs in the same beds with a marine fauna of a tropical climate.

VAUCHERIACEÆ.

General Characters.—The order is represented by a single genus *Vaucheria*, and is the only one among the *Siphoneæ* with distinct oogamous reproduction. Its simple, little differentiated thallus and highly developed type of reproductive organs, as well as the possession of non-sexual zoospores and a mode of vegetative propagation, mark it out from other

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multinucleate plants. The species occur not only in the sea, but even more plentifully in fresh water and in places that are merely damp. The description of the natural order below is based on its general characters, and is inclusive of those derived from fresh-water species.

The Thallus is simply a multinucleate filament, irregularly or dichotomously branched, and without farther differentiation. It forms much-branched, colourless holdfasts. The cell-wall is thin and the nuclei abundant in the protoplasm lining the walls. Sometimes crystals of oxalate of lime occur in the cell-sap. The chromatophores are oval and without a pyrenoid. Cross-walls occur only in connection with reproductive processes.

The Reproductive Organs.—The oogonia and antheridia are usually lateral outgrowths from a filament and occur side by side, though dicecious forms are known. The oogonia arise as round protuberances with a broad base, and gradually become more or less ovate and eventually cut off by a cross-wall at the base. The apex is generally papillate and the protoplasm becomes colourless here, and in this respect unlike the rest of the contents, which are coarsely granular and green, especially in the centre. The wall opens at the apex, and while the contents show a slight contraction, there is protruded a drop-like portion of a mucilaginous appearance. While this development is in progress the antheridium arises from the same filament as the oogonium and very near it. It is tubular in shape, and though sometimes straight is generally curved, and its cross-

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wall is formed, as a rule, at the curve and not at the base. In *V. synandra* several occur together on what has been called an "androphore," while in *V. de Baryana* and *V. piloboloides* the antherozoids escape by lateral openings in the antheridium. There is,

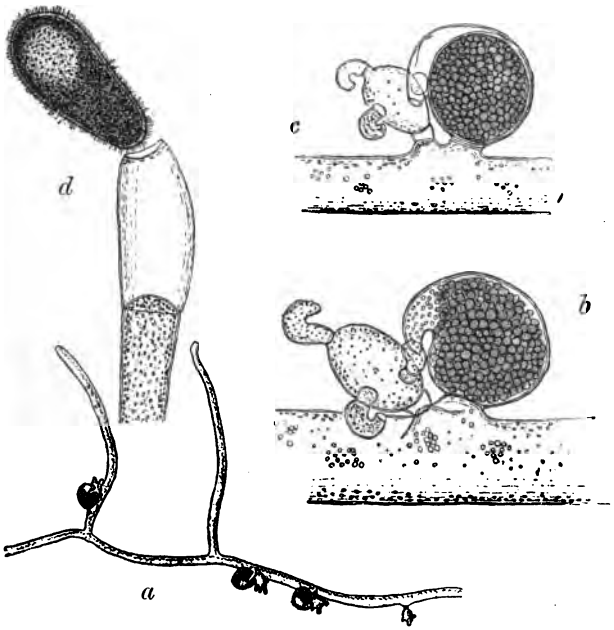


FIG. 34.—*Vaucheria synandra*. *a*, filament with oogonia and antheridia; *b*, oogonium with antheridia; *c*, later stage of same; *d*, escape of zoospore. Highly magnified. (After Woronin.)

in fact, considerable variety, of use in classification, in the forms of the antheridia. The contents have very little colouring matter, and break up into a large number of small, biciliated antherozoids with the cilia pointing in opposite directions, which escape

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through the bursting of the apex. They gain access to the oosphere by its apical opening and impregnate it. The oospore thus formed invests itself with a wall, assumes a brownish colour, and generally undergoes a period of rest before germination. The plants that result from this germination are commonly reproduced by non-sexual means for several generations of individuals before antheridia and oogonia are formed again.

Zoosporangia, usually slightly club-shaped, are produced by the formation of a cross-wall near the end of a filament. The contents of the cell so formed, which are rich in green colouring matter, gradually contract into an oval shape, and escape by the bursting of the wall at the apex. There is thus normally but one zoospore in each zoosporangium, and it is large and ciliated at all points, except in some cases the posterior portion. These cilia are in pairs, and immediately beneath each pair there is a nucleus near the surface, as if the whole body represented an aggregate of zoospores which have failed to separate. In the formation of zoospores in other *Chlorophyceæ*, there is usually one formed for each nucleus in the parent cell, and it is only natural to regard the case of *Vaucheria* in the light indicated, as pointed out by Schmitz, who first observed it. It is more than a mere case of preserving the multinucleate character of the parent cell, since there is this definite relation of nuclei to pairs of cilia. It is of interest in this connection to note that during the escape of this great zoospore it sometimes gets nipped in two by the wall in passing the opening, and

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each portion becomes a zoospore. The zoospore retains the character of its parent cell in respect of a cell-sap cavity, traversed by threads of protoplasm. A certain resemblance of this remarkable body to the *Volvocineæ* (fresh water) suggests inevitable speculations which may easily be made too much of. In the allied genus *Derbesia* (*Codiaceæ*) there are formed a number of zoospores in each zoosporangium —but before this the parent cell contains a large number of nuclei which unite with each other, and thus become reduced to a number equivalent to the number of zoospores.

The zoospores soon lose their cilia and settle down, becoming invested with a cell-membrane. They do not rest, however, more than a day or two at most, and germinate by the emission of one or more tubes. It happens in some species that antheridia and oogonia are occasionally formed on these filaments immediately after germination.

Motionless spores are produced by the formation of cross-walls near the apex and the abstriction of this portion, which first swells into an oval or globular form. It secretes a new cell-wall, and is set free by the dissolution of the original wall. In some cases such spores germinate soon, in most they rest before germinating. This spore-formation, like the more extensive formation of such bodies by segmentation of the thallus, is often caused by injury or unfavourable external conditions, and is more characteristic of the species inhabiting fresh water, which are moreover subject to the attack of rotifers (*Notommata*) giving rise to galls.

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The Geographical Distribution is general, and the best-known British marine forms are *V. dichotoma*, *V. synandra*, *V. Thureti*, *V. sphærospora*, and *V. litorea*.

CODIACEÆ.

General Characters.—The order is represented by the genera *Codium* and *Bryopsis*, differing in habit and mode of branching, but agreeing in the production

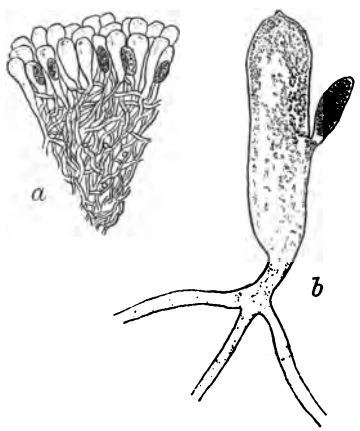


FIG. 35.—*Codium tomentosum*. *a*, part of section showing club-shaped cells of periphery with lateral sporangia highly magnified ; *b*, one such cell with sporangium more highly magnified.

of gametes of two sorts, between which conjugation, though it has not been observed, may yet be presumed with much probability to occur. *Derbesia*, also included here, is of more simple vegetative development, and possesses, so far as is known, but one kind

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of reproduction, viz. by zoospores. It is consequently an aberrant type, but its inclusion may be justified on grounds dealt with later.

The Thallus.—The beautiful feather-like fronds of *Bryopsis* recall the habit of certain species of *Caulerpa*, but between the genera there is little more than this superficial resemblance. Wille has stated that in old stalks of *Bryopsis* trabeculæ sometimes occur, but the observation is open to question. If established, it would certainly help in the elucidation of the position of *Caulerpa*, especially when taken together with the observation of Correns (p. 124) on the character of the cell-membrane. The thallus of *Bryopsis* consists of a single branching cell differentiated into rhizoids and erect shoots. The shoots consist each of a primary stalk, which either itself bears the ultimate lateral branches (which for convenience may be called leaves with apologies to formal morphology) or it may first branch repeatedly. The variations in this respect and in the occurrence of the leaves, whether opposite, alternate, secund, or in irregular spirals round the stalk, are characters of use in the discrimination of the species, though they are to be used with caution, since variation occurs within certain limits. The erect feathery fronds of a beautiful deep green are not only very graceful, but furnish objects of much interest for the microscopical study of the cell. In the middle of the cell is a vacuole, and the protoplasm lining the wall contains numerous nuclei and oval, flat chromatophores, each with one pyrenoid. *Bryopsis*, like *Derbesia*, *Vaucheria*, and *Caulerpa*, has all its filaments free, and not

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Fig. 36.—*Bryopsis Flanagani* natural size. (After E. S. Barton.)

interwoven like so many other multinucleate Algæ.

In the thallus of *Codium* two layers may be distinguished, though their component elements are all branches of the same cell. In the middle there is a densely interwoven mass of filaments which end outwards in club-shaped apices arranged perpendicularly to the surface. These club-shaped ends lie parallel to each other, and form a kind of pallisade tissue (Fig. 35). The spongy thallus so formed is of varying habit, either elongate and dichotomously branched (*C. tomentosum*), or in globular cushions, or flat and encrusting, without definite stalk and with very slightly developed rhizoids. The lumen of the cell is sometimes interrupted (apart from the formation of reproductive bodies) by plug-like thickenings of the membrane.

In *Derbesia*, the single filaments of the thallus show no differentiation of frond. They are dichotomously but sparingly branched, and are rarely, but with no regularity, septate in

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the older parts. The chromatophores are oval, and in some species contain a pyrenoid, in others not.

The Reproductive Organs.—In *Bryopsis* the gametes are produced on different plants within the lateral leaves, which undergo no modification to this end beyond the separation by a cross-wall or stopper from the stalk. They are of two sorts; the smaller male gametes being elongate and orange-coloured except at the anterior end, the female much larger and green, with a red spot between the green contents and the colourless portion. They are both biciliate. Sometimes the female gametes have a spike-like projection from the posterior end. In *Codium* the gametes are borne in lateral ovate sporangia (gametangia) arising from the club-shaped pallisade cells and lying among them, but never projecting beyond them (Fig. 35*b*). They are separated at the base by a cross-wall or stopper. The gametes are here also of two sorts, large green ones (female) and smaller yellow ones (male), both biciliate.

Conjugation has not been observed in either genus, but is extremely probable from the fact that Berthold's experiments in cultivating the green gametes were never successful, unless when these were mixed with the smaller ones. Analogy points also to this interpretation of their character. If this be so, we possess in the *Codiaceæ* a valuable link between *Vaucheriaceæ* and the other multinucleate orders. *Codiaceæ* would thus occupy to *Vaucheriaceæ* much the same position as *Cutleriaceæ* to *Fucaceæ* among the olive-brown seaweeds. As for non-sexual

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reproduction, however, the parts are reversed, since none is known in *Bryopsis* and *Codium*.

Went,[1] however, in studying *Codium tomentosum*, found both kinds of zoosporangia on the same individual plants. Sometimes the small gametes do not appear until after the dispersal of the larger ones—and they may be formed from the same basal cell. He never observed any union of the two sorts, and successfully cultivated the contents of the larger kind of gametangia or sporangia. But it is impossible to say in this case whether there had been conjugation or not.

In *Derbesia* we have only non-sexual reproduction, and, if the genus be rightly placed here, this fact also may have its significance, since *Derbesia* in other respects strongly resembles *Vaucheriaceæ*. The zoosporangia arise as lateral outgrowths from the filaments, and contain 8—20 zoospores with a fringe of cilia on the anterior end. As mentioned under *Vaucheriaceæ* the nuclei in the parent cell become reduced by union to the number of zoospores formed. However, it is plainly an aberrant type, and needs further investigation.

The Geographical Distribution.—Bryopsis occurs in all seas, but more abundantly in warmer waters. *Codium* also has an extensive range in the warm and temperate seas of the world. *Derbesia* belongs to the north temperate and tropical Atlantic (both European and American), and occurs also on the Australian coasts. All three genera are British, and (with *Vaucheria* and *Halicystis*) constitute our represent-

[1] *Vergrad. d. Ned. Botan. Vereeniging*, 1889.

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atives of multinucleate plants. The British species are *Bryopsis hypnoides* and *B. plumosa*, *Codium tomentosum*, *C. Bursa* and *C. adhærens*, and *Derbesia tenuissima*.

UDOTEACEAE.

General Characters. — The reproductive bodies (known only in the case of one genus, *Halimeda*) are zoospores produced within zoosporangia. It is not known whether they are zoospores or gametes in fact, since no observation has been made of their conjugation. The principal interest in the order is to be found in the vegetative part of the thallus, since the generic forms are not only of striking outward appearance, but of singular structure. The cohesion of the filaments composing the fronds is attained by their being interwoven (*Avrainvillea*), by incrustation of carbonate of lime (*Penicillus* and *Halimeda*), or by incrustation more or less partial with the addition of lateral haptera or holdfasts binding the filaments together (*Udotea*).

The Thallus.—In *Avrainvillea* (= *Fradelia*, *Chloroplegma*, *Rhipilia*, *Chlorodesmis*) the frond is of simple structure, consisting of unicellular filaments, repeatedly branched, and interwoven so as to form a stalked or sessile, fan-shaped, felt-like frond above and a dense mass of rhizoids below. The fan-like fronds are tough and spongy, and often lacerated at the edges. The filaments are dichotomously branched, and each branch is constricted at the base. In some of the species, the whole of the filament is constricted

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at short intervals, so as to resemble a chain of beads, though the constriction is not so deep as that would imply. This basal constriction is found also in *Penicillus*, and some species of *Udotea*. At the basal constriction in *A. comosa* there are sometimes formed

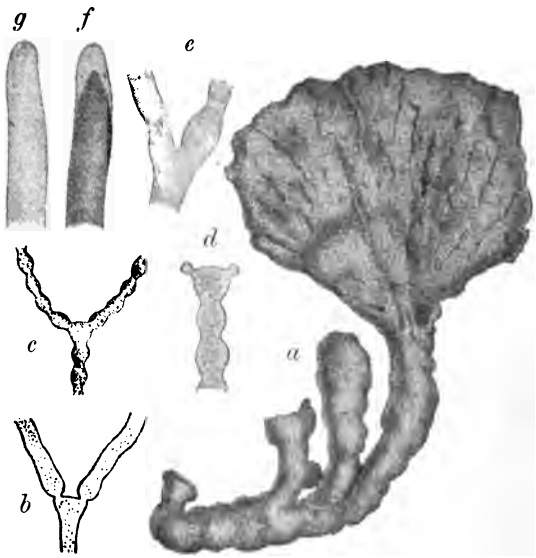


FIG. 37.—*a*, *Arrainvillea longicaulis* half natural size; *b*, frond filament of *A. Mazei*; *c*, ditto of *A. longicaulis*; *d*, ditto, showing beginnings of branches; *e*, filament of *A. comosa*, with stoppers; *g*, tip of filament of *A. papuana*; *f*, the same with dark brown contents. *b*, *c*, *d*, *e*, *f*, *g*, highly magnified.

stoppers like those of *Bryopsis* and *Codium*. In *A. comosa* the filaments of the frond are free, and in young specimens of *A. papuana* they are very little interwoven. The cell-wall is uniformly thin except in *A. longicaulis*, where it becomes (in the rhizoids) so much thickened in places as to obstruct the lumen

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of the cell. The chromatophores are rounded or polygonal, always with a clear central pyrenoid. Starch grains are very numerous, especially in the rhizoids, and are kidney-shaped in *A. papuana* and spindle-shaped in *A. comosa*. A yellowish or brownish colouring-matter is very abundant in the protoplasm and occurs very densely at the tips of the filaments, where it presents a dark resinous appearance. The rhizoids are less regularly dichotomous in their branching, and in most of the species enclose among the filaments masses of coral-sand, small shells, &c., so much so that the rhizoids of *A. papuana*, when drawn forth from the mud or coral-sand in which the plant grows, present the appearance of a cylindrical mass of crumbling mortar. In *A. longicaulis* there are formed rhizome-like, creeping bodies that connect large numbers of fronds. They are round like the stalks, and of the thickness of a finger. In this way so many plants are connected—all of them ramifications of a single multinucleate cell—that probably there is no parallel to it to be found in the plant world in respect of its dimensions.

Penicillus agrees in many essential respects of minute structure with *Avrainvillea*, such as the dichotomy of the filaments, but the plants do not outwardly resemble each other. The rhizoids are much alike, but the stalk is thickly incrusted with carbonate of lime, while from its summit the frond filaments wave free. Sometimes they are given off singly here and there from the surface of the stalk below the summit, but generally in a dense apical mass like a mop. In some species the filaments are

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free or almost free from incrustation, while in others each filament is thickly incrusted. In the latter case they are constricted at short intervals like a string of beads. *Penicillus mediterraneus* has a growth-form formerly known as *Espera mediterranea*, in which there is no stalk, but all the filaments are free. Similarly the species of *Avrainvillea* with free



FIG. 38.—*Penicillus capitatus* natural size.

filaments and no stalk (*A. comosa*) were formerly placed in a separate genus *Chlorodesmis*. A fossil genus *Ovulites* from the Eocene (Paris basin) has been placed here by Munier Chalmas, but though there is no doubt it is a calcified siphoneous Alga and does not belong to the Foraminifera as formerly thought, its position near *Penicillus* is not so certain.

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It might, with almost equal fitness, be placed elsewhere. Its remains are in the form of small egg-shaped bodies with a hole at each end, and each of these is taken by Munier Chalmas to represent the beads in the filaments of a *Penicillus*-like plant.

In *Rhipocephalus* there is an erect incrusted stalk giving off at intervals numerous small fronds also incrusted, composed of dichotomous filaments. It forms a transition to the next genus.

Udotea has the same fan-like, stalked fronds as *Avrainvillea*, but in this case they are incrusted, in some species very little, in others thickly. The filaments are little interwoven, but in addition to the incrustation they are bound together by numerous short lateral branches terminating in haptera or sucker-like holdfasts. The fronds in some species are beautifully zoned, and there is in nearly all a tendency, more or less marked, to proliferation at the margin. The round bodies, figured by Kützing, which have been taken to be zoosporangia, are probably of foreign origin.



FIG. 39. — *Rhipocephalus Phœnix* one-half the natural size.

Halimeda is the most singular of the group in the

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form of its fronds. These are chains of incrusted segments jointed together cactus-fashion, and the shape of the segments varies with the different species, but is usually more or less heart- or kidney-shaped or irregularly round. These chains usually arise from cylindrical incrusted stalks, and,

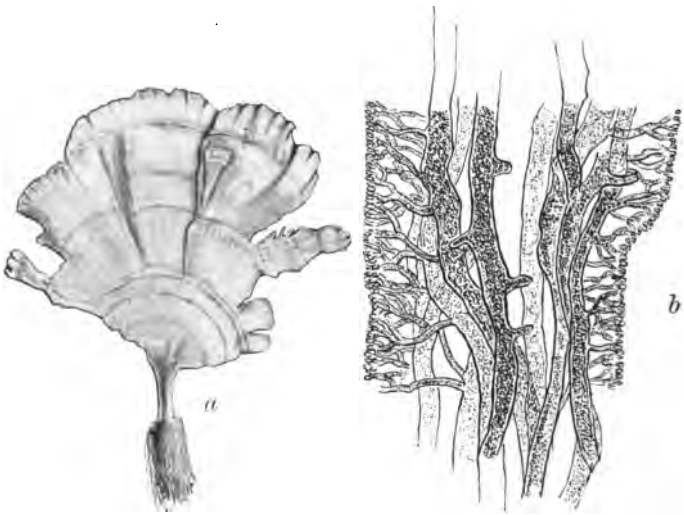


FIG. 40.—*a*, *Udotea Pavonia* half natural size; *b*, the same in longitudinal section highly magnified.

like the other genera, are firmly rooted by a mass of rhizoids. The filaments composing the fronds are dichotomously branched, but of irregular form. The central ones are large and elongated in the direction of the axis, while from them spring shorter ones passing outwards towards the margin, forming a kind of cortical zone (Fig. 41*b*).

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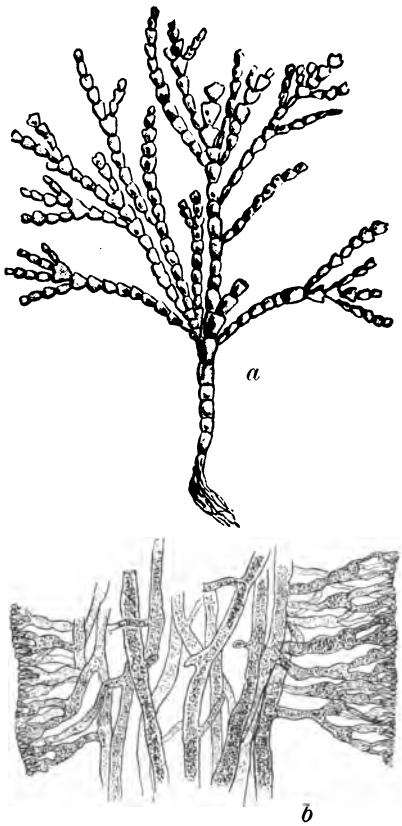


FIG. 41.—*a*, ***Halimeda monilis*** half natural size; *b*, the same in longitudinal section highly magnified.

Callipsygma is a genus of which only an imperfect description has been published. It appears to be related to *Avrainvillea* and *Udotea*.

A fossil Alga of Devonian Age, *Nematophycus*, has

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been placed in this group by Mr. Carruthers. It possesses stalks more than a foot in circumference, and must have been a colossal member of the group. Its filaments are entirely free from cross-walls, and are bound together by very fine lateral branches, though these do not appear to terminate in haptera, but rather wind round the larger main filaments.

The Reproductive Organs are known only in the genus *Halimeda*, and are zoosporangia producing biciliated zoospores. The zoosporangia arise from the margins of the flat fronds, and are round or pear-shaped bodies borne on branching filaments. They are green in colour and not separated by cross-walls from the filaments of the thallus. The zoospores are very small and green in the posterior part, hyaline at the ciliated end. They are produced in great numbers. No observation has been made of their possible conjugation or germination.

The genus *Codiophyllum*, placed here doubtfully by Wille, is identical with a red seaweed *Thamnoclonium*.

The Geographical Distribution.—The order is almost wholly tropical, though *Penicillus*, *Udotea*, and *Halimeda* have each one representative in the Mediterranean. All the genera except *Callipsygma* (of somewhat doubtful validity) are represented in the West Indies, while *Avrainvillea*, *Halimeda*, and *Udotea* are abundant also in the warm Indian Ocean, Malay Archipelago, and Pacific islands. *Penicillus* has not quite such a wide range, but occurs in the West Indies, Australia, and Moluccas. *Callipsygma* is known only from Australia.

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DASYCLADACEÆ.

General Characters.—The thallus consists of an erect axial cell with no cross-walls, bearing whorls of lateral branches, some hair-like and sterile, others of definite growth and fertile. The shoot is attached by rhizoids to its substratum. Reproduction is effected after the conjugation of gametes. The order is naturally divided into at least two sub-orders, viz. *Acetabularieæ* and *Dasycladeæ*.

Acetabularieæ.

The Thallus.—The erect axis bears at its summit a disc-like cap, consisting of radiating chambers, which in the species of the genus *Acetabularia* (as



FIG. 42.—*Acicularia Schenckii* natural size. (After Solms-Laubach.)

formerly defined) are united to each other laterally so as to form a firm disc. Other species were formerly placed under *Polyphysa*, but that genus is now

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joined to *Acetabularia*, and these are characterised by the radiating chambers being free from each other, and by other differences.

The best studied species is *A. mediterranea*, and a

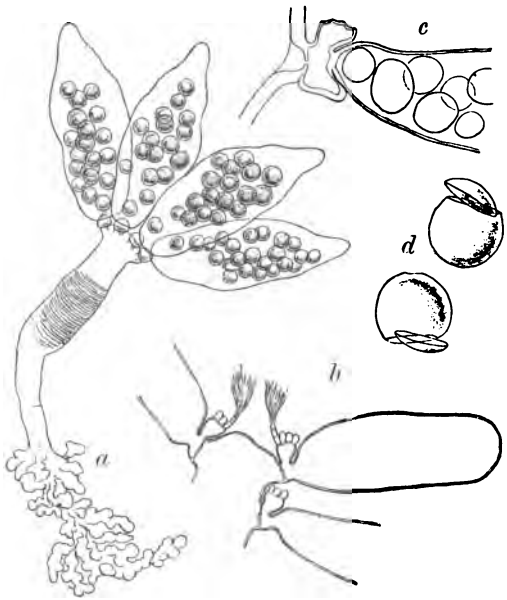


FIG. 43.—*a*, *Acetabularia exigua* decalcified (magnified); *b*, *Acicularia Möbii*, longitudinal section with two superposed caps; *c*, *Acetabularia Calyculus*, cap-ray with spores showing upper and lower coronæ; *d*, *A. exigua*, spores with lid. *b*, *c*, *d* highly magnified. (After Solms-Laubach.)

description of it will enable us to understand the variations displayed by the others. It has an erect stalk six to nine centimeters high, with a cap about a centimeter across, strongly calcified and partitioned into a number of regular radial chambers,

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which unite in the centre above the insertion of the stalk. This central area immediately above the stalk is covered with a flat circular membrane above, and is surrounded, where the radial chambers are given off, by a continuous circular cushion (Fig. 43*c*), the *corona superior*. This corona consists of as many segments as there are radial chambers, and each segment bears the scars of hairs that have fallen off or remain incompletely developed. In like fashion below the marginal radial chambers there is another cushion, the *corona inferior* (Fig. 43*c*), corresponding with the upper one, but bearing no hair-scars. A lower but less-marked cushion exists, but it gradually becomes merged in the central area. Each marginal ray stands in communication with the relative segments of the corona (superior and inferior), and these in turn are marked off from the central area by a fold of the membrane with a central opening, which frequently becomes closed by subsequent thickening. The radiating chambers bear the spores (gametangia).

In the species formerly placed under *Polyphysa* (which has been merged into *Acetabularia* by Graf zu Solms-Laubach), the sporangial rays are completely free from each other, and not united into a firm disc, as in *A. mediterranea*. They are quite uncalcified in some species and very slightly so in others and have no corona inferior, while the corona superior is represented by free knobs bearing hairs.

A. mediterranea takes several years to attain the formation of a fertile cap. In the first season no cap is produced, but merely erect stalks, with occasion-

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ally irregular protuberances at the tip. The plant dies down, and the lower part of the stalk, closed with a membrane at the base, remains alive during the winter, and may be described as consisting of two portions, viz. the foot, calcified and irregularly branched, and a basal, rhizoid body. This basal body increases with age, and acts as a storehouse of reserve-material for further growth. In the following year a cap without spores is produced, while the stalk, before this happens, gives rise to one or more whorls of branched hairs. These hairs are not calcified, and are soon thrown off, leaving only rings of scars on the stalk of the cap-bearing plant. After giving rise to several sterile plants in succession, eventually a fertile cap is borne.

This production of whorls of hairs is interesting, not only in throwing light on the homology of the sporangial rays, but in relation to the neighbouring genus *Halicoryne*, which possesses alternate whorls of fertile and sterile branches. The sterile whorls consist of repeatedly multisect hair-tufts developed in groups of eight; but they soon fall off, and leave round scars on the stalk. Between these on the full-grown plant there are sixteen-branched whorls of a different kind—the sporangial rays, which are completely free. Each ray is furnished on its upper surface near the base with a small protuberance bearing one or two diminutive rudimentary hairs, recalling the corona superior. Interesting also in this connection is the fact that *Acetabularia crenulata*, in the normal course of its development, and not as a monstrosity, produces several caps in succession

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above each other (Fig. 44). *Halicoryne* is, in fact, a better representative of the *Acetabularieæ* than the disc-forming *Acetabularia*, since it supplies us with a link to the other *Dasycladaceæ*, from which it is distinguished, however, by the alternation of fertile and

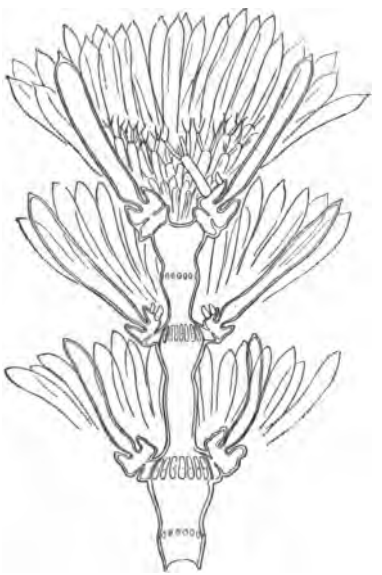


FIG. 44.—*Acetabularia crenulata* with several caps in longitudinal section highly magnified. (After Solms-Laubach.)

sterile whorls, in addition to the more important characters of the sporangia. The genus *Chalmasia* (like the former genus *Polyphysa*) has no corona inferior, and while closely resembling *Acetabularia* in most respects, agrees completely with *Halicoryne* in the structure of the spores. In *Halicoryne* their mem-

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branes are strongly calcified and stratified. *Acicularia*, which has both corona superior and inferior, is distinguished from *Acetabularia* by the fact that its spores are strongly calcified (those of *Acetabularia* are free from incrustation), and adhere in clusters. *Acicularia* contains both living and fossil forms. The latter are *A. Andrussowi* and *A. miocenica* from the Miocene and *A. pavantina* from the Eocene.

The Reproductive Organs.—The life-history has been followed in great detail in *A. mediterranea*. Within the marginal chambers the spores (gametangia) are produced in considerable numbers. They rest from one to three months after extrusion, and then opening by a lid at one end emit the gametes. The gametes are biciliated, of equal size and same shape, and with a red spot. They conjugate usually in pairs, and not only so, but in fours or fives, sometimes laterally sometimes in reversed position; but conjugation takes place only between gametes derived from different gametangia. After conjugation they do not immediately settle down, but remain in a state of movement with the cilia in pairs still vibrating. The zygote, so formed, eventually gives rise to a new cap-bearing generation, after a rest of about five months.

If we apply the theory of alternation of generations to the life-history of *Acetabularia*, we must regard the product of the zygote, viz. the cap-bearing plant, as the non-sexual one, terminating in the production of spores within its radial chambers. The sexual generation is represented by the spores which without any vegetative manifestation become them

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selves gametangia, bearing gametes which conjugate, and so form a zygote.

The Geographical Distribution.—The *Acetabularieæ* are a tropical and subtropical order. Of the fifteen species of *Acetabularia*, one however occurs in the Mediterranean and *A. Peniculus* on the West Australian coast. They occur in all tropical seas. *Halicoryne* has two species, one (*H. Wrightii*) in the China sea and the other (*H. spicata*) on the shores of New Caledonia. *Chalmasia* has only one species, *C. Antillana*, and *Acicularia* is represented alive only in the warm Atlantic (West Indies and South America).

Dasycladeæ.

The Thallus.—This sub-order is characterised by the persistence of the whorls of hairs and by there being no distinction between fertile and sterile whorls—they are all fertile, except locally in the joints of *Cymopolia*—and by the gametangia being terminal members of the lateral branches, except in *Botryophora* where they are of lateral origin on these branches.

In *Dasycladus* the shoot is nowhere incrusted, and consists of a short erect axial cell without constrictions or cross-walls, attached to the substratum by a holdfast, and clothed with whorls of branches, about twelve to each whorl. These are again branched in whorls several times, each successive whorl diminishing outwards in length and in the number of branches. At the apex of the ultimate whorl there is produced a single globular sporangium

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(gametangium) on a short stalk surrounded by the end branches. In *Botryophora* there is also no incrustation, and the habit is similar but more lax, the plants being larger and the branches not so densely packed together. The sporangia are lateral and occur several together on the base of the branches. They contain a large number of spores with membranes, which may be gametangia, but no observation of their germination has been made. There is only one species, which was originally described under *Dasycladus*, and very probably that will prove to be its true position. *Neomeris* has an incrusted shoot of otherwise similar character to *Dasycladus*. The lateral branches bifurcate and end each in a swollen tip. These tips are arranged in rows of facets externally, forming a sort of outer cortex to the shoot.

At the bifurcation of the lateral branches and between them, occupying morphologically the summit of the original lateral branch, there is a single oval sporangium, with one spore as to the development of which nothing is known. *Bornetella* differs from *Neomeris* in the branches being in two or three successive whorls and in the sporangia being of lateral origin, and containing several spores. *Cymopolia* is of very different habit since the main shoot, the axial cell, is repeatedly branched dichotomously. It consists of chains of cylindrical, incrusted portions, separated from each other by short, not incrusted, joints in which the branching has its origin. The apex of each branch has a terminal tuft of hairs like a brush. At the incrusted portions

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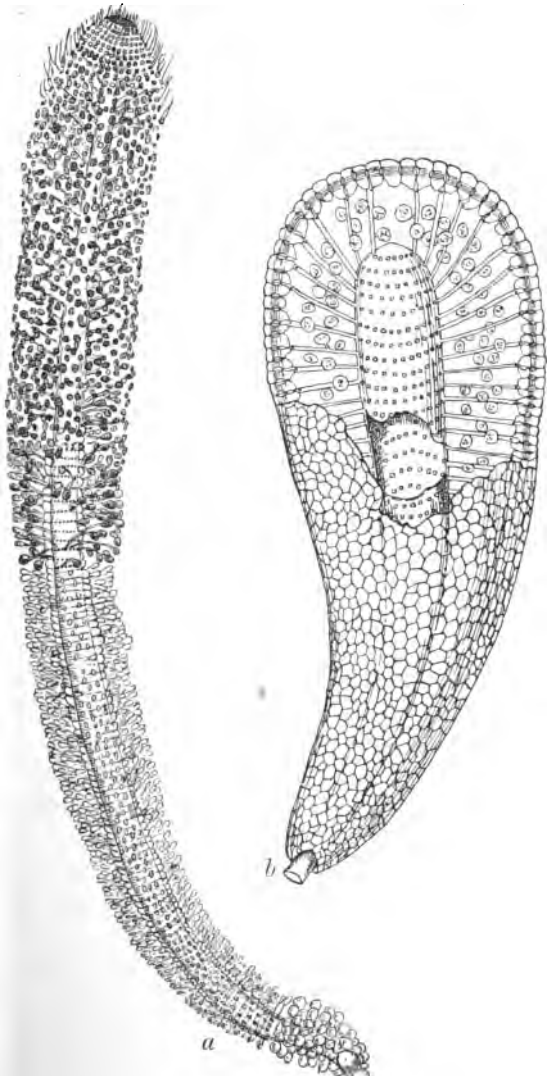


FIG. 45.—*a*, ***Neomeris annulata*** magnified ; *b*, ***Bornetella oligospora*** magnified (After Solms-Laubach.)

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there are borne the fertile whorls, each with a secondary whorl and a terminal sporangium in the middle. The ultimate whorl of these lateral branches, overtopping the sporangia, form a kind of cortex (as in the last genera), but without definite facets externally. The space between them and the axial cell is originally of slimy consistence, but becomes the seat of incrustation. At the joints there are no fertile whorls and the lateral branches are here simple and decrease in length from below upwards. It is a similar formation which bears the terminal tuft of hairs. No observation of germination has been made.

A number of fossil genera, such as *Decaisnella*, *Haploporella*, *Dactylopora*, *Dactyloporella*, *Uteria*, and *Polytrypa* from the Eocene, and *Munieria*, *Gyroporella* and *Triploporella* of Cretaceous age are certainly nearly related to the forms just described.

The Reproductive Organs.—Dasycladus is the only genus in which the gametes have been observed. We have seen that in *Acetabularia* the gametes unite only with those from other gametangia, but in *Dasycladus* the matter is carried a step farther, since the gametes are here incapable of conjugation with others from the same plant, and indeed they conjugate only with those of particular plants, not with any other indiscriminately. It appears from this observation that though these gametes are apparently all alike, there yet resides within them a definite character indicating a difference of sex, though this is not determinable by us from their structure.

Judged by itself alone, *Dasycladus* appears to pre-

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sent us with a case of a spore (gametangium) borne not in a sporangium as in *Acetabularia*, but free on its branch. One may regard this spore, however, in the light of a sporangium which omits to form spores and itself gives rise directly to gametes, and this view is much strengthened by comparison with the case of *Botryophora* and *Bornetella*, where there is an actual sporangium, with spores of similar origin, though we do not know from observation what the fate of these may be. *Dasycladus* by itself appears to exhibit perpetual production of sexual generations, while in *Acetabularia* it is this generation that remains undeveloped, and is represented only by the spores (gametangia). Such interpretations, however, must remain purely speculative until further light is thrown on the matter by an examination of the life-history of such forms as *Botryophora* (so near *Dasycladus*), *Neomeris*, *Bornetella*, and *Cymopolia*.

The Geographical Distribution, like that of *Acetabularieæ*, is in tropical and subtropical seas. *Dasycladus* has one species occurring in the Mediterranean and the Canary Islands. *Botryophora* also has one species confined to the West Indian region. *Neomeris* has several species, one in the West Indies, others in Madagascar, the Malay Archipelago, and the tropical Pacific. *Bornetella* is Australian, and occurs also in the tropical Pacific. *Cymopolia barbata* occurs in the West Indies, the Canary Islands, and has been recorded from Cadiz, but not from the Mediterranean, while *C. van Bossei* represents the genus in the Malay Archipelago.

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VALONIACEÆ.

General Characters.—There is scarcely any Order to which it is more difficult to assign distinctive general characters, owing to the much varied structure of the vegetative organs and our ignorance of the reproductive processes in most of the genera. The thallus ranges in variety from a single large cell with rhizoids up to forms of complex structure with stalk and frond. The cells of the thallus are frequently linked together by haptera or holdfasts. The reproduction by zoospores described for *Microdictyon* and *Anadyomene* certainly needs minute re-investigation, but that of *Siphonocladus* and *Valonia* stands on a firmer basis of observation. In *Valonia* spores with cell-membranes arise by free-cell-formation within the great lumen of the cell, but their germination has not been observed. The following types indicate the character of the thallus, and exhibit a series connecting the multinucleate Algæ with the other *Chlorophyceæ*, or at all events pointing to such a connection.

The Thallus.—The most simple type is that of *Valonia ventricosa* (Fig. 46*a*), which consists of a single cell, generally varying in size from that of a gooseberry to a hen's egg. This enormous cell, much the largest cell of isodiametric shape known to us, is attached to its substratum by rhizoids at the base, and presents a uniform green appearance, except on the cessation of its vegetative life, when the protoplasm with the chromatophores, which had lined the wall,

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shrinks into the great lumen of the cell-sap cavity and leaves the plant as a translucent sphere. In this condition it frequently parts company with its attachment and floating to the surface is drifted ashore. It is common in the West Indies, and reaches Bermuda, where the plants are often drifted ashore in this translucent state, and are called "sea-bottles" by the inhabitants. *Halicystis ovalis*, which resembles this plant in shape, but is much smaller, occurs in the Clyde Sea area (and extends from western France to the Faroes and Scandinavia). Its systematic position is uncertain, since we know nothing of its reproduction, but so far as may be judged by the structure of its membrane, which shows none of the striation and very little of the stratification of *Valonia*, by its chromatophores, which have no pyrenoid, while those of *Valonia* possess one in many cases at least, and by the substitution of a sucker-like disc for rhizoids, it must be placed apart from *Valonia*. Schmitz suggests that its vegetative structure recalls the freshwater *Botrydium* most closely, and is mainly distinguished from it by the absence of rhizoids. However, this is true also of a comparison with *Valonia*, and until we know its reproduction any speculation must carry little weight.

In other species of *Valonia* there occurs a remarkable form of branching, if it may be so termed. Small portions of protoplasm and chlorophyll gather opposite more or less definite parts of the membrane, generally near the apex, and separate themselves from the rest of the contents by the formation

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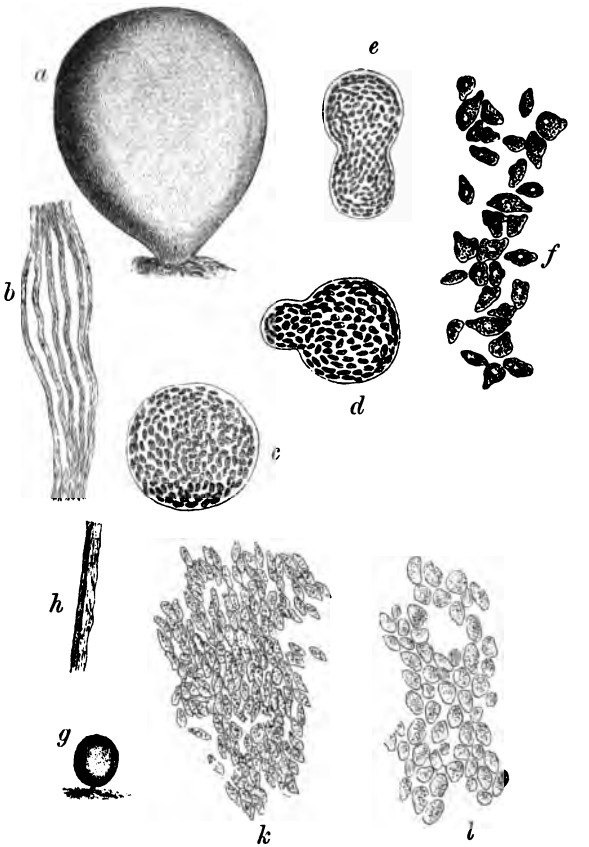


FIG. 46.—*a*, *Valonia ventricosa* slightly reduced; *b*, section of wall; *c*, *d*, *e*, reproductive bodies; *f*, chromatophores *b*, *c*, *d*, *e*, *f*, highly magnified; *g*, *Halicystis ovalis* natural size; *h*, section of wall; *k*, *l*, chromatophores *h*, *k*, *l*, highly magnified. (Ex. *Phyc. Mem.*)

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of a membrane of the form of a watch-glass. This cell then proceeds to grow out from its parent cell, and assumes a similar shape. The process is then repeated, and by this means a thallus is produced, generally with irregular branching, but sometimes having the appearance of successive dichotomous or verticillate branching from the apex of each generation of cells.

Dictyosphæria favulosa in its early state is an irregularly globular mass of large cells (Fig. 47*c*), the interior of the mass becoming hollow with its growth. It eventually bursts, and the thallus is then irregularly lobed. It consists of numerous cells in several layers, all of these being bound together by sucker-like holdfasts, short where the cells are closely packed, and long-stalked where they are more loosely aggregated. There are remarkable internal spines projecting from the cell-membrane into the cell-cavity (Fig. 47*h*). *D. sericea* has a different arrangement of holdfasts, but the main points of structure are the same. Wille describes the origination of the cells of *Dictyosphæria* within a mother cell. This may be the case, but an examination of many early stages of *D. favulosa* does not bear it out. However, it would be in harmony with what is known of *Valonia*.

The placing of *Blastophysa* among the *Valoniaceæ* is uncertain. The plants are green, very irregular, much lobed cells with long colourless hairs. It is certainly multinucleate, but its reproduction is unknown, and its vegetative characters inadequate for determining its true position.

Siphonocladus is a simple, minute, multicellular

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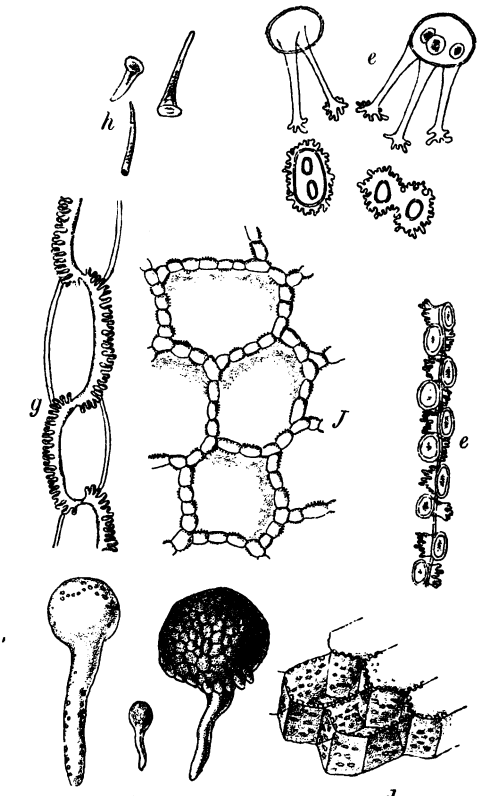


FIG. 47.—*Dictyosphæria favulosa*. *a*, *b*, *c*, young specimens; *d*, diagram of cells joined by haptera; *e*, haptera in side and surface views; *f*, *D. sericea*, surface view of frond; *g*, bordering cells with haptera; *h*, internal projections from cell-walls of *D. favulosa*. Variously magnified. (Ex. *Phyc. Mem*).

branched type, which leads on to forms with a higher differentiation of thallus. In *Apjohnia* there is a main stalk with numerous rugose constrictions and

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with no cross-walls, giving off rhizoids below and dichotomous branches above. *Chamaedoris* has a similar stalk, with its branches given off in a great terminal tuft—in habit like *Penicillus* in this respect. It appears very probable that the stalk is persistent and renews its crop of branches, both in this genus and at all events in some of the species of *Struvea*.

The large species of *Struvea* are among the most beautiful of Algæ. At the summit of the long rugose stalk without cross-walls there is borne a flat frond, through which the stalk is prolonged as a mid-rib. This mid-rib gives off opposite branches, which are again pinnately branched, and in some species these are similarly branched again and again. Where these pinnæ meet they are all bound by sucker-like haptera (Fig. 48*e*), and the frond presents the appearance of a lovely piece of lace. *S. plumosa*, *S. macrophylla*, and *S. pulcherrima* are the largest and finest species. Only three specimens of *S. macrophylla* have been found, two of them being in the herbarium of Trinity College, Dublin, and one in the British Museum. *S. pulcherrima* is even more rare, one specimen, not quite complete, being in the British Museum, and a fragment in the Edinburgh herbarium collected at the same time. The more slender forms have stalks unmarked by rugosities. The forms described as species of *Spongocladia* were long puzzling. They are dense wefts of interwoven filaments, with walls so much thickened in places as to obliterate the cell-lumen. They grow in intimate association (Symbiosis) with sponges, and assume to some extent the habit of these animals. It has

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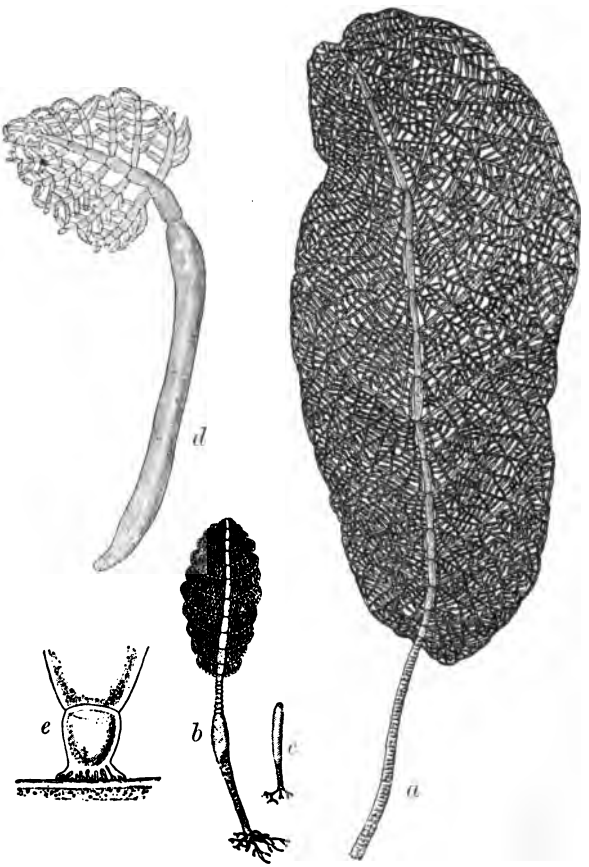


FIG. 48.—*a*, *Struvea macrophylla* slightly reduced; *b*, *S. plumosa* slightly reduced; *c*, young plant of same; *d*, *S. tenuis* magnified *e*, one of the haptera by which the filaments are bound together highly magnified. (Ex. *Annals of Botany*).

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been made quite clear by Mrs. Weber van Bosse that certain forms of *Spongocladia* are mere growth-forms of *Struvea delicatula*, transformed by this remarkable association with a sponge. This proof has a further interest as regards *Struvea*. No reproductive organs of *Struvea* are known, but Areschoug, who originally described *Spongocladia*, has figured what appear to be zoospores germinating *in situ* within the filaments of *S. vaucheriæformis*.

In *Microdictyon* we have similar net-like fronds, but without a stalk. The frond, which is of prostrate habit and of indefinite margin, is attached by short rhizoids. A closely-allied genus, *Boodlea*, instead of forming a flat network, has branches running indefinitely in all directions, each branch bound to its neighbours by haptera like those of *Struvea*. We have therefore a sort of network extending in all directions, and not in one plane like *Microdictyon* and *Struvea*. In *Anadyomene* the flat thallus recalls *Struvea* in being traversed by main branches, but the spaces between these are wholly filled with the cells of lateral branches, and there is therefore no network.

Though the thallus of *Dictyosphæria*, for example, may be utterly unlike such a form as *Struvea* in habit, there is in reality very little dissimilarity in structure. The binding of the cells together by haptera to form a tissue is common to both extreme forms; in the one case the cells remain isodiametric and unbranched, in the other they are more or less elongate and definitely branched.

The Reproductive Organs.—Zoospores are produced in *Valonia*, *Siphonocladus*, and possibly in *Microdictyon*

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and *Anadyomene*, not in special zoosporangia but in any of the ordinary thallus cells. The zoospores are bi-ciliated, with a hyaline anterior end and a red spot. Nothing is known of their further history.

In *Valonia ventricosa* (Fig. 46) there arise by free cell-formation a large number of spores with cell-

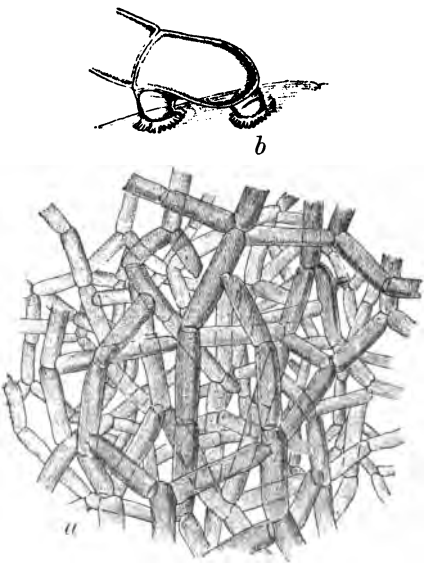


FIG. 49.—*Boodlea coacta*. *a*, thallus filaments; *b*, two haptera highly magnified.

membranes. They do not all arise simultaneously, since in some specimens comparatively few spores are to be found, while a considerable amount of free protoplasm remains; in others again the spores are very numerous and the amount of unused protoplasm is a mere trace. Somewhat similar spores

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PLATE IV.

1. Ulva Lactuca.

2. Enteromorpha intestinalis.

3. Cladophora rupestris.

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are produced in *Siphonocladus* as a result of injury of the thallus.

The Geographical Distribution.—The distribution of the order is mainly tropical—only the genera placed here with hesitation — *Halicystis* and *Blastophysa* reaching the North Atlantic and North Sea. *Valonia*, with about fifteen species, is of wide occurrence in the warmer seas; *Apjohnia*, with two species, is found in Australia and at the Cape; *Siphonocladus*, with several species, in the Mediterranean and in tropical seas; *Chamædoris* (one species) in all tropical seas; *Dictyosphæria* (two species) in the West Indies and Australia; *Struvea* (six species) in the tropics for the most part; *Boodlea* (one species) in the Pacific; while *Microdictyon* and *Anadyomene*, with six or seven species each, are also mainly tropical.

CLADOPHORACEÆ.

General Characters.—The thallus is always a row of single cells in some cases branched, in others simple, and since these cells contain each several nuclei, it is very difficult to say where the dividing line is to be drawn between *Cladophoraceæ* and *Valoniaceæ*—between the old order *Siphoneæ* and the other *Chlorophyceæ*. In the typical *Cladophoraceæ* the filaments, whether branched or simple, grow erect in tufts, but in *Gomontia* the habit of the whole plant is modified by its living within the substance of shells which the filaments perforate. Reproduction is effected by the conjugation of equal gametes, and by

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zoospores each with four cilia. Vegetative propagation also takes place.

The Thallus.—In *Chætomorpha* the thallus remains unbranched, in *Rhizoclonium* there are very short branches, while in *Urospora* there are mere lateral outgrowths from the cells, not cut off by cross-walls; in *Cladophora* the thallus is densely branched, the branches being given off at the upper part of the cell, just below the cross-wall separating it from the one above. The base, which is attached to the substratum by a holdfast, is in some cases, *e.g Cladophora rupestris*, much strengthened by the growing together of a number of rhizoid filaments. The filaments of *Gomontia*, which inhabits the shells of molluscs, penetrating their substance very densely, are less regularly branched, and the cells become irregularly swollen, sometimes more or less beaded. The whole thallus may be easily isolated by placing a fragment of the green-stained shell in Perenyi's fluid (see p. 30).

The number of nuclei in each cell varies considerably, and the chromatophores also vary in shape, but are mostly perforated and flat, or net-like, with abundant pyrenoids.

The Reproductive Organs.—Gametes are produced by both *Cladophora* and *Urospora*. They arise within the vegetative cells in large numbers, and escape by a round hole; they are bi-ciliated and have a red spot. They are all exactly alike in appearance, and conjugate in pairs. The zygote germinates at once in *Cladophora*, and after a period of rest in *Urospora*. Zoospores are known in all the genera except *Rhizo-*

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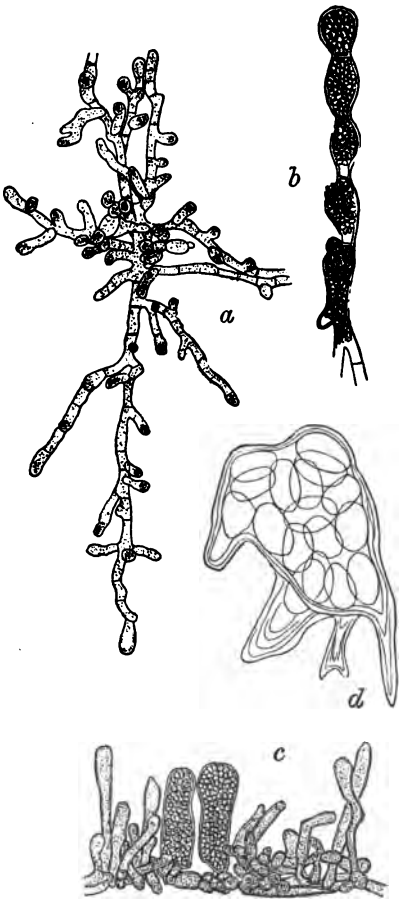


FIG. 50.—*Gomontia polyrhiza*. *a*, young plant decalcified; *b*, filament of older plant; *c*, section showing filaments with sporangia; *d*, sporangium with non-motile spores. Variously magnified. (After Bornet and Flahault.)

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clonium. They are of similar origin to the gametes, but have four cilia. In *Urospora* they have a long tail, and looked at endways, they are four-sided with sharp angles, but they appear to possess the power

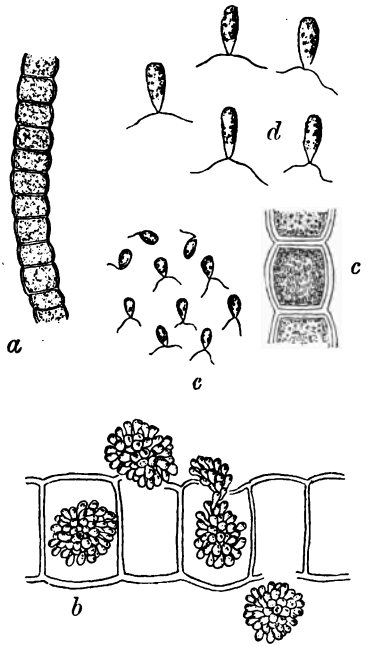


FIG. 51.—*Urospora penicilliformis.* *a*, filament; *b*, escape of gametes; *c*, part of filament more highly magnified than *a*; *d*, zoospores; *e*, gametes highly magnified. *c*, *d*, *e*, after Areschoug.

of altering their shape somewhat, so that the sides are now concave, now convex.

In *Gomontia* the sporangia are larger than the ordinary vegetative cells, and the zoospores have only two cilia. There are also produced in this genus

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motionless spores within large sporangia. These spores, which are round and provided with a membrane, do not germinate in the ordinary way but become themselves small plantlets with a rhizoid attachment. These either soon give rise to a filamentous thallus, or, becoming enlarged, are transformed into new sporangia, the actual outcome of which has not yet been observed.

In *Urospora* and *Rhizoclonium* there is a method of vegetative propagation by the separation of vegetative cells densely packed with contents. In *Urospora* the filament breaks up first into multicellular parts and eventually into single cells. These either germinate directly or, after surrounding themselves with thick walls and resting, produce zoospores. In *Rhizoclonium* the process is simply that of the cells becoming rounded and dropping off; they germinate by the production of a filament in all cases.

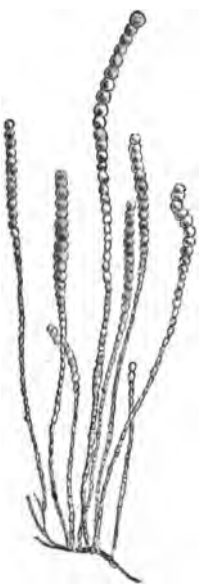


FIG. 52. — *Chætomorpha Darwini* (reduced).

The Geographical Distribution. —*Cladophora* has a world-wide distribution in both salt and fresh water. *Chætomorpha* is also extensively distributed, but mostly in the sea. *Rhizoclonium* has a similar distribution to *Cladophora*. All three genera are represented by numerous species, many of them

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established on insufficient grounds. *Urospora* and *Gomontia* have as yet been recorded only in Europe, but the latter has probably a much wider area. All the genera are represented in British seas.

ULOTRICHACEÆ.

General Characters.—The genera here brought together are usually classified as follows: *Ulothrix* under *Ulotrichaceæ*, and *Chætophora*, *Bolbocoleon*, *Entoderma*, *Epicladia*, *Phœophila*, *Acrochæte*, and *Acroblaste* under *Chætophoraceæ*. The limits between these two orders are, however, hard to define, and they do not appear to rest on very weighty characters. Both are much more largely represented in fresh-waters with numerous generic types not occurring in the sea, and a discussion of the propriety of treating these orders as one or separately is out of place here. There is certainly no strong reason for separating by ordinal division the genera dealt with here. The thallus is a simple branched or unbranched cell-row, with one nucleus in each cell, and the reproduction is by the conjugation of equal gametes with two cilia, and non-sexually by zoospores with two or four cilia. Vegetative forms of propagation are also known.

The Thallus.—In *Ulothrix* the thallus consists ordinarily of a single cell-row, attached at the base by a holdfast. The cells are all equally capable of division, except the basal one, which is generally more elongate than the others. *Chætophora* is very

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densely branched in all directions without possessing any main axis. It forms gelatinous cushions or irregularly globular masses. *Bolbocoleon* has a creeping thallus of rows of cells without erect branches, though the cells exhibit an upward protuberance. Small conical cells, ending upwards in fine bristles, and with very little colouring matter,

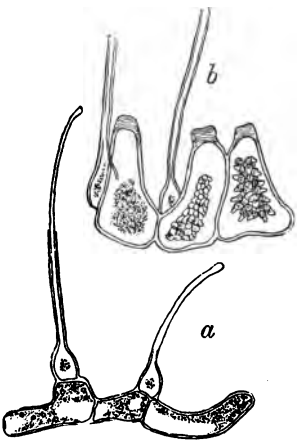


FIG. 53.—*Bolbocoleon piliferum*. *a*, filament with hairs; *b*, cells with zoospores. Highly magnified. (After Pringsheim.)

occur on and between the ordinary vegetative cells. *Entoderma* grows as an endophyte within the membranes of other Algæ; it is irregularly branched, and sometimes is developed after numerous cell-divisions into a kind of tissue-mass. The divisions as a rule, however, take place only in the pointed terminal cell. *Epicladia* is a creeping epiphyte on the surface of *Flustra* and other Bryozoa, and in many respects

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resembles *Entoderma*. Its thallus is densely branched, and the branches eventually grow together and form a continuous plate. *Phœophila* and *Acrochæte* are small epiphytic forms on other Algæ, allied to *Bolbocoleon*, as also is *Acroblaste*, which grows on stones and shells. The latter has both creeping and erect filaments.

The Reproductive Organs.—Conjugation of gametes is known in *Ulothrix* (as well as in *Bumilleria*, a fresh-water genus). The gametes are formed in the ordinary vegetative cells, and escape by a side opening. They are ovate in shape, have two cilia and a red spot. They conjugate in pairs, and occasionally in threes, and form a zygote. (The gametes have been observed to germinate without conjugation after coming to rest, but the filaments are more slender than those emitted by the zoospores.) The zygote increases in size and its membrane becomes thicker; after a period of rest its contents divide up into a number of zoospores which germinate after swarming. *Phœophila* has gametes with four cilia, which conjugate with their posterior ends. *Ulothrix* is reproduced non-sexually by zoospores, one to four in number, produced in the vegetative cells, as the gametes are. They are larger than these and have each four cilia. In *Ulothrix implexa* zoospores are sometimes formed which do not escape, but surround themselves with a membrane, and eventually germinate after the decay of the wall of the mother-cell. *Chætophora* also possesses zoospores with two cilia, and these sometimes fail to escape and behave like those of *Ulothrix implexa*. *Entoderma*, which, like

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Chætophora and the remaining genera, is without gametes so far as has been observed, produces zoospores in the vegetative cells. These escape through a hole in the membrane of the cell, and of that of the host-plant as well. They have no red spot, and since no observation has been made of the number of their cilia or of their germination, &c., it is quite possible that they may prove to be gametes. *Epicladia* and *Bolbocoleon* possess also zoospores produced in the ordinary cells; in the latter case, also, no observation of the number of cilia has been made.

Acrochæte, which has short upright branches arising from the creeping filaments, forms zoospores in the terminal cells of such branches as have no bristles. In *Acroblaste*, also, the terminal cells of the upright branches become zoosporangia.

The Geographical Distribution is world-wide in the fresh-waters, and very insufficiently known in the sea. The species of *Ulothrix* are in great confusion, but one certain form, *U. implexa*, is marine, and occurs in British seas. Only two species of *Chætophora* are marine (neither of them British), both of them in the Arctic sea. *Bolbocoleon*, *Epicladia*, and *Entoderma* are all small genera, and occur in British and neighbouring seas. *Phæophila*, *Acrochæte*, and *Acroblaste*, also small genera, have not yet been recorded on British coasts. There are a number of other genera, such as *Ctenocladus*, which occur in brackish water, but are scarcely marine.

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ULVACEÆ.

General Characters.—The *Ulvaceæ* are among the first seaweeds that meet the collector's eye on reaching the shore, since they grow for the most part at high-water mark. The thallus is either a flat green expanse of tissue, lobed irregularly, or hollow, green, tubular and unequal. There are no special sporangia, but the ordinary vegetative cells of the thallus act as the parent cells of gametes, which conjugate, and of zoospores with four cilia.

The Thallus.—In its most simple form, that of *Monostroma*, the thallus consists of a flat layer of cells, one cell thick, at least in the upper portion; in *Ulva* and *Letterstedtia* uniformly two cells thick, and in *Enteromorpha* also two cells thick; but these layers soon separate, and produce a hollow space between them, giving rise to the tubular forms that are characteristic of the genus. The greater part of the basal cells of the *Ulvaceæ* grow out into filamentous processes which become irregularly interwoven, and, while serving as a fixing organ to the substratum, add to the thickness of that part of the thallus.

While a certain degree of branching of the thallus occurs in *Enteromorpha*, it is only in *Letterstedtia* that lateral foliar appendages—if they may be so called—of definite growth occur. These subsequently fall off from the older parts of the main shoot, leaving it bare and irregularly toothed at the margin. *Pringsheimia* is a very minute epiphyte

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on other seaweeds, consisting of a single layer of cells.

Usually there is no definite or characteristic arrangement of the cells, but in *Ilea*, a genus much



FIG. 54.—*Letterstedtia insignis*. Reduced.

resembling *Enteromorpha*, and sharing its tubular character, there are groups of four cells arranged in quadrants, and in *Enteromorpha* longitudinal rows of cells may be traced. The cells contain each only

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one nucleus, and the disc-shaped chromatophores one pyrenoid.

The Reproductive Organs.—Gametes with two cilia are produced by the ordinary vegetative cells in *Ulva*, *Enteromorpha*, *Monostroma*, and *Pringsheimia*, and their conjugation in pairs has been observed. There is no apparent difference to be seen among them. The zygotes so formed germinate by the production of a short cell-row in *Ulva*, and the formation of a globular body in *Monostroma bullosum* by cell-divisions in all directions. This globular body after enlargement forms a hollow bag, and eventually bursts, when the thallus resembles the other species of *Monostroma*. The zoospores are of similar origin to the gametes, are larger, and have each four cilia. In *Monostroma Wittrockii* the zoospores (?) have only two cilia; but it is possible that they may be in reality gametes which germinate without conjugation. However, *Pringsheimia*, of which the gametes are known, has definite zoospores with two cilia.

The Geographical Distribution is world-wide, and extends to fresh-waters in the case of *Monostroma* and *Enteromorpha*. *Ulva* enters brackish waters in all parts of the world, but *Letterstedtia*, which is purely marine, has a very restricted range, occurring only on the coast of Natal (and Australia ?). *Ilea* is an inhabitant of brackish waters in Europe and North America, and is often known by the name of *Capsosiphon*. All the genera except *Letterstedtia* occur in British seas. Species of *Enteromorpha* form the "grass" which causes to a very large extent the fouling of the bottoms of ships.

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PROTOCOCCACEÆ.

General Characters.—This is a very large order, very sparingly represented in the sea. Except in European seas, however, the marine forms have been little studied, and it is probable that many more types will be added in time, especially after a more extended examination of the floating Algæ of the open ocean. The thallus is unicellular, and the cells are never associated intimately to form a tissue or definite group obeying a common law of growth. There are no cell-divisions during vegetative life. The plants are either stipitate or free, and never motile, unless of course in the zoospore stage. The conjugation of equal gametes has been observed, and also non-sexual reproduction by zoospores.

The Thallus.—*Chlorochytrium* and *Chlorocystis* inhabit the tissues of other plants, the former mainly flowering plants in fresh-water or on land, but also seaweeds, and the latter exclusively seaweeds. The cells are globular, oval, or irregular in shape, and the main vegetative difference between the genera appears to be in the shape of the chromatophores, and the fact that *Chlorochytrium* has many pyrenoids while *Chlorocystis* has but one in each chromatophore. *Chlorocystis Cohnii* inhabits the tissues of many seaweeds, and *C. Sarcophyci* causes deformities of the thallus of *Sarcophycus*. *Halosphæra* is a beautiful globular form, living free in the ocean, and forming a considerable constituent of the plankton or floating

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flora of the warm and temperate Atlantic and Mediterranean. *Characium*, a genus of about thirty species, of which only two are marine, is a stalked form with ovate cells, and *Codiolum* and *Sykidion* more or less resemble it vegetatively.

The Reproductive Organs.—Chlorochytrium possesses gametes which escape from the mother-cell embedded in a mucilaginous mass, and conjugate

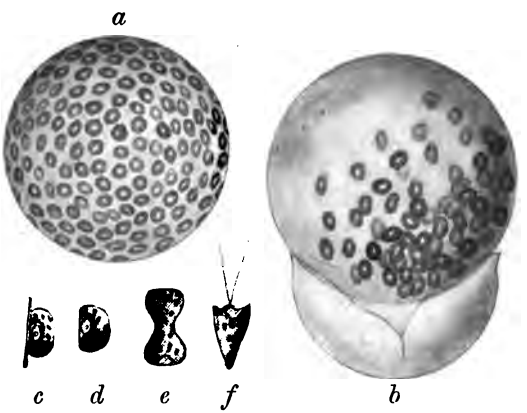


FIG. 55.—*Halosphæra viridis*. *a*, showing the protoplasm gathered round the nuclei and lining the wall; *b*, the outer membrane, cast off after enlargement of the sphere, the daughter-cells separated from the wall; *c*, *d*, *e*, stages in the development of zoospores; at *e*, the hour-glass shape is preliminary to division into two; *f*, zoospore highly magnified. (After Schmitz).

before leaving it. The zygote remains motile by means of the four cilia (of the two bi-ciliated gametes), and eventually on coming to rest surrounds itself with a membrane, and penetrates the tissue of the host-plant by means of a short germ-tube. *C. dermatocolax*, which inhabits *Polysiphonia* and *Sphacelaria*, and *C. inclusum*, which

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lives in the tissues of *Sarcophyllis*, have been insufficiently studied, and probably are identical with *Chlorocystis*. In *Chlorocystis* the zoospores (or gametes) leave the mother-cell without any mucilaginous envelope. No gametes are known in *Halosphæra*, and zoospores are formed after the division of the nucleus into numerous nuclei. Round these nuclei the protoplasm and chromatophores assemble and form plano-convex bodies, each of which divides by constriction into two zoospores. These are conical in shape, with a slight protoplasmic projection at the base, from which the two cilia arise. *Characium* has zoospores showing difference of size, but all with two cilia, and these escape by an apical opening of the cell. In *Sykidion* the zoospores are all of the same size, but before their formation the cell-contents are enclosed within a new membrane. *Codiolum* has zoospores with two cilia, and also motionless spores.

The Geographical Distribution of marine *Protococcaceæ* is very imperfectly known. All the genera occur in British seas, except a doubtful genus, *Pleurocapsa*, recorded from the Adriatic. Nearly all the marine forms are known only in European waters, except *Chlorocystis Sarcophyci*, which is Australian. The pelagic forms are widely distributed, but too little known to permit of a definite statement.

PLEUROCOCCACEÆ.

General Characters.—This order, like its allies, is more largely represented in fresh-waters than in

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the sea. The cells of the thallus are motionless, and may occur singly or in colonies. There are no gametes or zoospores, and reproduction is exclusively a matter of cell-division in the ordinary vegetative manner. A number of *Pleurococcaceæ* are generally regarded as reduced forms allied to other orders.

The Thallus of *Prasiola* is a membrane consisting of a single layer of which the cells are rectangular, while in *Palmophyllum* a rounded, lobed, and zoned frond is formed of roundish cells embedded in a gelatinous mass. The *Pleurococcaceæ* of which the cells are not associated in definite colonies, but separate on division, are represented in the sea by the genus *Zoochlorella*. This remarkable genus inhabits the bodies of various invertebrate animals, such as *Radiolaria*, &c., in which they have long been known as the "yellow cells." It has been contended by Brandt, Geddes, and others that there is here a true symbiosis or mutual partnership between the plants and their hosts, and that the animals are nourished on the products of assimilation by the plants, as in the case of the lichens, where the fungal portion subsists on the algal gonidia. It appears, however, from recent research, that while this is no doubt true enough, it is not the whole matter, and that the symbiotic relation is more partial or even occasional than was at first supposed. It has been demonstrated by Beyerinck that *Zoochlorella* may live (in his experiments for several weeks) outside the bodies of animals, and Famintzin has observed their multiplication in a nutritive solution. An extensive literature has arisen on this subject generally.

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However Cienkowski, one of the first to observe these "yellow cells" and to indicate their algal character, long ago based his argument on the observation that they continued to live and multiply long after the death of the animal; and Geddes, as well as Brandt, fully established their algal character by a series of minute observations made simultaneously and independently.

Reproduction is, as has been said, by the separation of vegetative cells.

The Geographical Distribution of the order is world-wide. *Zoochlorella* has a wide distribution in the warmer seas, while *Prasiola* occurs in fresh-waters, as well as in the sea, throughout the world. *Palmophyllum* is confined to Europe. *Prasiola* is the only genus recorded in British seas, though the order is represented by many genera in the fresh-waters of this country.

PERIDINIEÆ.

General Characters.—Judged by our present knowledge of this order, it occupies a position on the borderland between the plant and animal kingdoms, while the balance of evidence certainly leans towards our regarding them as plants. Some of the forms, like *Ceratium*, are certainly plants. They occur in very varied forms, always free and never attached, except to each other in chains, as in *Ceratium Tripos*, both in fresh-waters and the sea, and have, some of them, membranes, others not. They pass through a ciliated motile phase and a resting

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stage, and their reproduction is always by mere cell-division. The reported conjugation may be regarded as extremely doubtful.

The Thallus.—The membrane consists of a substance nearly related to cellulose, sometimes impregnated with carbonate of lime (though this is not the case in *Ceratium*), and its growth has been described as peculiar, and not to be adequately explained by apposition or intussusception. In the marine forms, at all events, the protoplasm consists of two zones, the outer one being hyaline towards the outside and granular towards the inside. In this granular portion are embedded the chromatophores and fatty drops and plates. The interior body of protoplasm is very finely granular, and contains the nucleus and vacuoles. The chromatophores support three different substances, viz. phycopyrine, peridinine, and chlorophyll.

In some of the fresh-water forms an animal-like nutrition has been described, and green Algæ (*Chlamydomonas* and others) are stated to have been ingested and partly digested. In such forms no chromatophores occur, and the starch present must be the fruit of such captures. It is apparent from such observations, and from others, that very diverse organisms have been gathered together under this order.

Reproduction is always by division, and since it appears to occur in the most varied way among the fresh-water forms—in some cases during the motile phase, in others during the resting stage and after encystment—this fact lends support to the view that the order is not very coherent.

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The Geographical Distribution of the marine forms is principally in the temperate waters of the ocean, more abundantly in coastal waters than far from land. Vast banks of *Ceratium* occur on the British

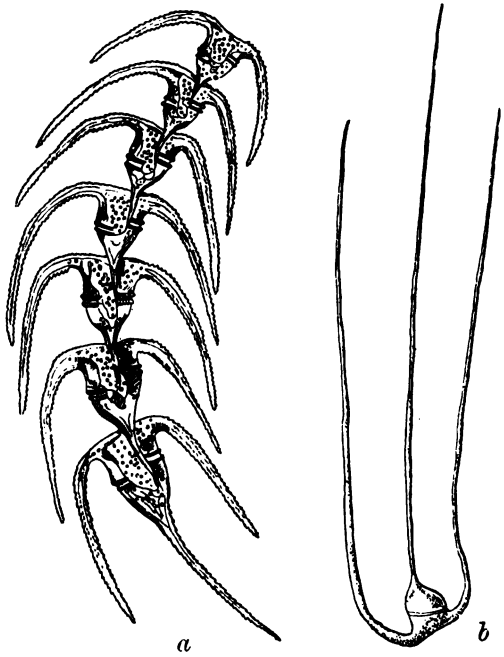


FIG. 56.—*a*, *Ceratium Tripos* (in catenâ), after J. Murray; *b*, single *Ceratium* Both highly magnified. (After Schütt.)

coasts, causing the waters to be brightly luminous at night. They form, with the Diatoms, a very large proportion of the primary food of marine animals. The occurrence of *Ceratium Tripos* in catenâ (Fig. 56)

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has been observed only in the open ocean, far from land. In coastal waters they occur separately.

The genus *Pyrocystis* (*P. noctiluca* and *P. fusiformis*), observed by Dr. John Murray during the *Challenger* Expedition, and subsequently by other naturalists, is

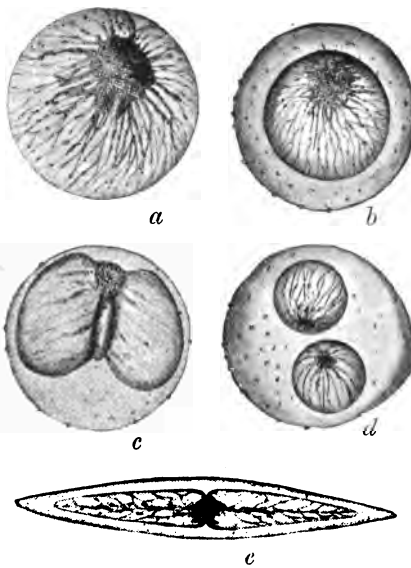


FIG. 57.—*a*, *b*, *c*, *d*, *Pyrocystis noctiluca*; *e*, *P. fusiformis* highly magnified. After J. Murray.)

a very puzzling one, and, owing to our insufficient knowledge of its life-history, very hard to place in a satisfactory systematic position. It is a tropical form, and to it was attributed the most brilliant displays of luminosity of the sea during the *Challenger* Expedition. It bears a certain degree of resem-

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blance to the encysted condition of some *Peridinieæ* on the one hand, and on the other is not without a suggestion of likeness to the Desmids, an order of beautiful unicellular Algæ known only in fresh-waters. The forms are globular, 0·6 to 0·8 mm. in diameter, and spindle-shaped, with a colourless membrane, showing some resemblance to that of *Ceratium*. The nucleus is eccentric, and connected by fine strands of protoplasm with the protoplasm that lines the membrane. The chromatophores are small yellow plates. *Pyrocystis* thus differs entirely from the Desmids in the colouring matter and disposition of the protoplasmic contents. The indication of division in Fig. 57, *c*, *d*, is the only known mode of reproduction.

Coccospheres and Rhabdospheres.

These names have been given to exceedingly puzzling organisms which occur in vast abundance in the ocean. There appears to be little room for doubt that they are calcareous unicellular Algæ. They occur in all surface and subsurface waters of tropical and temperate seas beyond the influence of coast waters, and are often found entangled in the protoplasmic matter of *Foraminifera* and *Radiolaria*, in the stomachs of *Crustacea* and *Salpæ*, as well as free in large numbers in the water. The Rhabdospheres are tropical and the Coccospheres temperate, though the latter occur within the tropics as well, but not so abundantly.

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Their broken-down parts, called Rhabdoliths and Coccoliths, occur in the globigerina oozes, and they form a not inconsiderable part of deep-sea deposits, except those laid down in polar and subpolar seas. The Rhabdoliths and Coccoliths are known from the deposits of the ancient cretaceous seas. Their minute investigation in the living state is one of the most

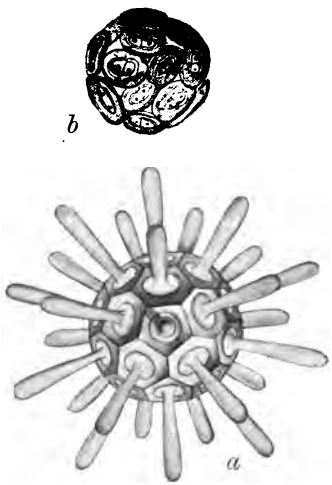


FIG. 58.—*a*, Rhabdosphere; *b*, Coccosphere highly magnified. (After J. Murray.)

important researches yet to be undertaken in marine botany. (See p. 28.) "There is considerable variety both in the form and size of Coccospheres and Rhabdospheres, some varieties having the component parts (Coccoliths and Rhabdoliths) much more compactly united into a sphere than others. The interior of the spheres is perfectly clear when

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examined fresh from the surface, and becomes coloured brown with iodine solution, but with iodine and sulphuric acid no blue colour was observed. They were never observed to colour with carmine solution. When the calcareous parts are removed by dilute acids a small gelatinous sphere remains, in the outer layer of which the Coccoliths or Rhabdoliths were embedded." ("*Challenger* Reports." Narrative, vol. i. p. 939.)

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SUB-CLASS III

DIATOMACEÆ

THIS great group, consisting of, it is estimated, some 10,000 species, and universally distributed in the waters of the globe, has been treated sometimes as a Natural Order allied to the *Desmidieæ* (confined to fresh-waters), and sometimes as a sub-class, with the view of marking its peculiar characters, within the range of which there exists astonishing variability of form without losing any of the essential points of character that distinguishes the group. They are given here the value of a sub-class, in recognition of the weight of this argument, while the familiar name of *Diatomaceæ* (which implies a Natural Order) is retained for overwhelming reasons of convenience; and their description is framed for similar reasons on the plan adopted for Natural Orders, since a subdivision of them would lead to an extended systematic treatment quite beyond the scope of this book. While their colouring-matter resembles that of the *Phæophyceæ*, they are otherwise much more nearly related to orders placed

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under *Chlorophyceæ*, notably the *Desmidieæ*, the *Peridinieæ* (which have also a peculiar colouring-matter), and, it may eventually prove, the calcareous Coccospheres and Rhabdospheres. The Diatoms have a very extensive literature of their own, from the fact that their great beauty and universal distribution have made them in a singular degree the objects of special study.

General Characters.—The plants are very minute unicellular, with the walls strongly silicified, and composed of two overlapping halves or shells called *valves.* The valves overlap, the one above the other at the edge, much as the lid of a cardboard box overlaps the box itself, and this overlapping edge is called the *girdle.* Each individual, consisting of two valves, is called a *frustule* in the special literature of the subject. The colouring-matter is chlorophyll masked by a brownish substance called *diatomine,* readily soluble in alcohol, and resembling the peculiar colouring-matter of the *Phœophyceæ.* Many Diatoms are endowed with a power of independent movement. The reproduction affords highly distinctive characters. After a series of successive bipartitions, involving a gradual diminution in the size of each new generation, the original dimensions are regained by the formation of an auxospore by various methods, some of them involving conjugation, but not between motile gametes.

The Thallus.—The individual Diatoms live either singly or in chains, and they may be wholly free, or borne on gelatinous stalks, or enveloped in a gelatinous mass. The fresh-water forms do not

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reach so great a size as the marine, the former rarely attaining one third of a micro-millimetre in length, while some marine forms approach three micro-millimetres. They may be distinguished in the mass by their brownish colour. The infinitely varied markings on the siliceous valves afford systematic characters, and are fully displayed after cleaning—*i.e.* the removal of the organic matter by calcination, or by treatment with nitric acid. Owing to the silicified membranes, the plants when once formed are incapable of further growth, though alterations of volume occur by the sliding of one valve over the other to the extent of the breadth of the girdle. It is impossible by mere verbal description to convey an adequate idea of the variety and beauty of the forms assumed by Diatoms, or of the fine sculpturing of their valves. In describing them it is the practice to denote the aspect in which the girdle side is presented as the girdle or zonal view, and the aspect which displays the surface of the valve as the valve view. When the latter is presented the central portion is frequently free from fine markings, and may be traversed longitudinally by a line called the *suture* or *raphe*, while *nodes* or *nodules* representing thickenings occur at each end, or in the centre as well.

Each Diatom contains a nucleus, and the colouring-matter occurs in plates or bands of more or less regular form; drops of oil are frequently also present. A resting condition sometimes occurs, in which pairs of new valves are formed within the original ones. Such states are called *craticular states*, and they appear to correspond to those con-

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ditions observed among *Chlorophyceæ* in which resting cells are formed by the contraction of the protoplasm and the thickening of the membrane. It is plain that, owing to the firm siliceous membrane, such a course is not open to the Diatoms, and the craticular state—the formation of new valves within the old ones—is the only resource, when a resting condition is called for, to prevent the drying up of the contents.

The movements of Diatoms have long been a puzzle, and various explanations have been advanced to account for them. This spontaneous movement of the free forms takes place with considerable rapidity and force, and is always backwards and forwards in the direction of their longer axis, sometimes stopping and then going on with a jerking movement, or proceeding more steadily in creeping fashion. This movement is never a free-swimming motion through the water, such as zoospores possess, but is always a movement along some fixed substance with the surface of which the shell is in contact, and it never takes place when the girdle-side is thus in contact. Naegeli ascribed this movement to osmotic currents, while Ehrenberg explained it by the protrusion of cilia or of a pseudopodium through the so-called suture or raphe (on the valve side). This observation has not been confirmed, but one proposed by Max Schultze is not unlike it, and appears to be probable enough. He supposes that a small portion of the protoplasm emerges through this suture and effects the movement. In favour of this view, which has not, how-

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ever, been established by direct observation, is the fact that most of the Diatoms possessing such a power of movement possess also longitudinal sutures, and it is supported by the observation that fine particles of matter (not motile by themselves) suspended in the water, on coming in contact with the membrane, are set in motion along the suture. However, no one has so far demonstrated the protrusion of any protoplasm at this place. That these movements take place with considerable relative force is shown by the observation of Donkin, who saw one species push away another at least six times its size, while other observers state that they have seen this greatly exceeded. The speed of the movement when compared with the rapid dartings of ciliated organisms is slow. The Rev. William Smith estimated the rate at about four hundred times a Diatom's length in three minutes.

Reproduction.—Diatoms multiply by successive bipartitions. The actively vegetating cell increases slightly in volume, and the two valves are slowly pushed out until the overlapping girdle remains in that position, but no more. The protoplasm then divides into two, and two daughter-cells are formed, not separated by a membrane in the ordinary way, but each new cell forms a new valve on the plane of division. The edges of the new valves fit into the girdle of the old valves of the parent cell, and these old valves overlap the new ones. Each daughter-cell thus possesses two valves, one newly formed and overlapped by the old one. The cells either separate and become free, or they remain in contact, and

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after successive divisions of the same kind, and always in the same direction, form a chain. Since

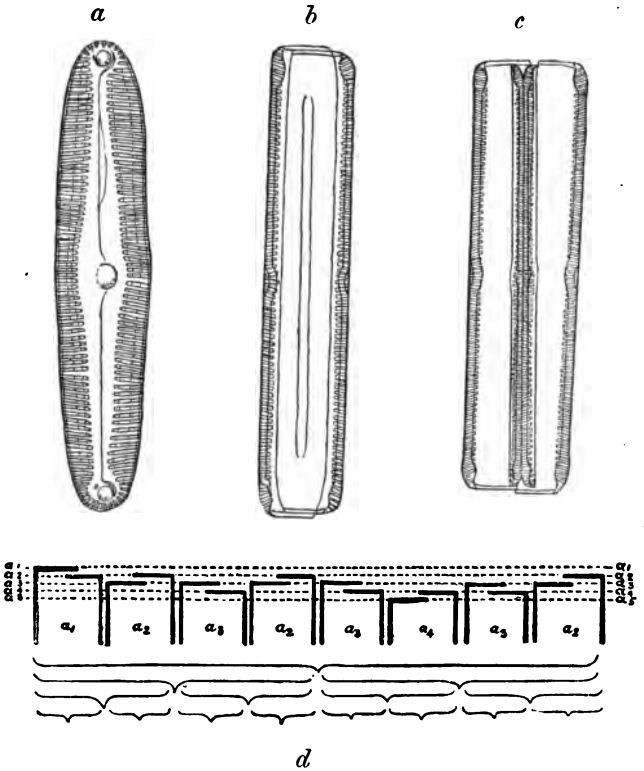


FIG. 59.—*Pinnularia viridis*. *a*, valve view; *b*, girdle view; *c*, the new valve has forced the girdle apart highly magnified; *d*, diagram of successive divisions of a Diatom. (*a*, *b*, *d*, after Pfitzer.) (*P. viridis* is a fresh-water form.)

every fresh division leads to the formation of new valves, the edges of which are within the girdle of

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former ones, it necessarily follows that every succeeding generation becomes smaller by just as much as the thickness of the membrane at the girdle, since, once formed, the Diatoms do not subsequently increase in size. The character of *size* frequently used by certain students of Diatoms must therefore be fallacious, and no doubt the inordinate multiplication of species in this group is partly due to its use.

When by this process, repeatedly carried out, a certain minimum diminution of size is reached, the original stature is regained by the formation of an auxospore. This may be formed in one of five different ways. (1) In the most simple form the valves open and the contents (generally, but not always, protected by a gelatinous envelope) emerge and increase in volume. The auxospore so formed soon acquires a thin membrane which is not silicified (the *perizonium*). Two siliceous valves are then formed, first one and then the other, within this membrane, enclosing all the contents, and it is noteworthy that these first valves, while possessing all the ordinary characters of the species, exhibit slight differences in the membrane from that of the daughter-cells, subsequently produced by division from this parent form in the manner described. (2) Instead of one auxospore, two may be formed by the division of the contents of the cell, and these two naked cells emerge from the separated valves and develop each into an auxospore. (3) An auxospore may be formed after conjugation. Two Diatoms secrete a common gelatinous envelope; the contents

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emerge from the valves and unite to form one body, which then grows into an auxospore. There seems to be some doubt whether there is here a true conjugation—whether these two cells are true motionless gametes and the product a zygote. (4) This process may be gone through, but without union. The two cells give up their contents, which lie side by side unclothed with a membrane, and either close together or separated by a layer of the gelatinous envelope. Each develops independently into an auxospore. (5) Two auxospores may be formed by a pair of Diatoms, which on emerging from the old valves divide each into two. Each pair of the four cells thus formed conjugate and form an auxospore. Regarding all these processes, it appears to be fair to assume that conjugation, or rather union, whether between one pair or two pairs, is the normal process of forming an auxospore, and that the other cases are parthenogenetic, where a pair produce auxospores together without conjugation, or where one produces two auxospores by itself, or where one similarly produces a single auxospore. The simplest form of all is common; so is the case of two Diatoms forming their auxospores without conjugation, and of two combining to form one by conjugation, though not so frequent as the others. The case of one Diatom forming two auxospores is known in only one form, *viz. Rhabdonema arcuatum;* and the last case, where two Diatoms divide and the daughter-cells conjugate, each pair giving rise to an auxospore, is recorded for *Epithemia Zebra* only. The mode of formation of

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auxospores varies within one genus at least, viz. *Cocconeis*.

The Geographical Distribution.—Diatoms are dis-

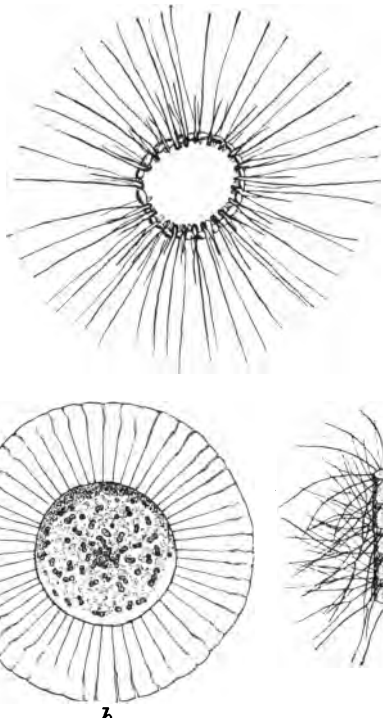


FIG. 60.—Pelagic Diatoms. *a*, *Chætoceras secundum*; *b*, *Planktoniella Sol*; *c*, *Bacteriastrum varians* highly magnified. (After Schütt.)

tributed in extraordinary profusion in the sea, in fresh and in brackish waters. and the species found in any of these situations are peculiar to it. The

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stipitate forms occur attached in slimy masses to Algæ, &c., and the free forms as a fine yellowish-brown scum on muds, or floating free in the surface and subsurface waters of the ocean, both coastal waters and those of the open sea. Just as the Rhabdospheres are tropical, and the Coccospheres and *Peridinieæ* characteristic of temperate tracts of the ocean, the Diatoms are found in greatest abundance in the colder waters of the northern and southern oceans, though they occur in all seas. They greatly outweigh all other pelagic plants in the colder waters. Sir James Ross's Antarctic Expedition discovered a great tract of ocean bottom in the southern ocean composed of diatomaceous ooze, *i.e.* the siliceous valves of dead Diatoms. Here, as elsewhere, the *Challenger* Expedition discovered an enormous abundance of living Diatoms in the surface tow-nets. South of latitude 50° the tow-nets were sometimes so filled with Diatom scum "that large quantities could be dried by heating over a stove, when a whitish felt-like mass was obtained." As this surface life perishes, the dead siliceous walls are rained down on the bottom to form the diatomaceous ooze.

They are found abundantly in shell-fish and crustacea, which use them as food, and also in the digestive tracts of fishes, and they undoubtedly are the most important ingredient in the vegetable pastures of the sea which support the whole of the animal life in it. They are very abundant in guano, into which they have entered from the intestinal canals of birds living on marine animals.

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They are not only engaged in forming oceanic deposits at the present day, but the fossil diatomaceous earths of Tertiary and Quaternary age are witnesses to their activity in past ages. The first occurrence of fossil Diatoms is in the chalk, and here, illustrating the persistence of the type, there are preserved species still existing in the waters. The extensive fossil deposits which are used as polishing powders (tripoli), in the manufacture of dynamite (Kieselguhr, &c.), and for other purposes, are interesting from the fact that though many species occur in them, one is always predominant, and it, or at most a few, form the mass of the particular deposit. All these fossil forms belong to genera and a large number of them to species now living. Some deposits have been laid down in fresh-water, others in salt-water, and the latter contain species that are still marine. The so-called edible earths of China and Japan, of Siberia, Lapland, &c., which are mixed with meal and so eaten, are of diatomaceous origin.

The earlier rocks have been very carefully searched, notably the Silurian, for fossil Diatoms, but without any trustworthy record. Castracane has stated that he found several species in the ash of English coal, but though he claims to have used precautions, the record is open to doubt, since an exhaustive and fruitless search has been made in many coals by very careful observers. The fact that Castracane's Diatoms are fresh-water forms now living adds to the doubt, from the possibility of a mistake in manipulation thus suggested, in spite of what we know of the persist-

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ence of such forms. It has been conjectured that the forms known as *Bactryllium* from the Trias may have been ancestors of the Diatoms, but perhaps there is less to be said and more to be doubted on this point.

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SUB-CLASS IV

RHODOPHYCEÆ, OR FLORIDEÆ

THE *Rhodophyceæ* or red Algæ are, in almost all cases, seaweeds. A few genera (*Batrachospermum*, *Lemanea*, *Tuomeya*, and *Balbiania*) belong to fresh-waters exclusively, where they occur for the most part in running streams, while a few other genera (*Chantransia*, *Hildbrandtia*, *Caloglossa*, and *Bostrychia*) have representatives in both fresh-waters and the sea. The thallus is always multicellular, of very diverse forms, and is composed of branching cell-filaments, either separate and free or congenitally united in their development. This union is effected in some cases by a merely gelatinous envelope, but is generally brought about by a very tenacious intercellular substance which binds the filaments so closely that the whole body becomes parenchymatous in appearance. The filaments increase in length by apical growth, only the terminal cell dividing. This cell is sometimes larger than the others, and sometimes indistinguishable from them in size. Intercalary growth takes place only by the extension of the

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individual cells, not by their transverse division, or by their median longitudinal division. Portions of the margins of the individual joint-cells may however be cut off by dividing walls, and these then develop into lateral branches. As this process may happen but once, or many times, simultaneously or in succession, varied modes of branching of the cell-filaments are produced.

Each cell of the filament is provided with a central pit in the cross-wall, and since such pits do not occur in the marginally cut-off cells, their presence or absence enables us to trace in a tissue the genetic connection of the individual cells with their neighbours. However, this frequently becomes complicated by the occurrence of secondary pits, formed subsequently between individual cells of the thallus. The pits are not open pores, permitting free passage of cell-contents such as nuclei and chromatophores, but they are closed by an exceedingly thin membrane. On both sides of this closing membrane there is a comparatively thick plate of a dense substance, recalling in its characteristics the mucilage-masses of the sieve-tubes of the higher plants. These plates adhere firmly to the closing membrane on both its sides, one in each cell, and they are connected with each other by numerous cords which perforate the closing membrane, mostly round the margin of the pit. The plates stand in direct connection with the protoplasm lining the cell-wall and are, in fact, so coherent with it, that they may be regarded as transformed or rather differentiated protoplasm locally covering the pit. However, it is probable that a thin

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layer of protoplasm covers them in turn. The cords which thus perforate the closing membrane establish a connection between adjoining cells, and though they do not admit of migrations of cell-contents in bulk, they may be used for the transference of dissolved substances. However, it is supposed that their main function is to transmit dynamic influences, while the plates are the receivers of such stimuli.

While the composition of the thallus of the *Rhodophyceæ* is effected typically by the congenital union of cell-filaments in which subsequent intercalary divisions do not occur, it happens in isolated cases that such divisions occur in an exceptional manner. They occur with regularity in certain Corallines, and in the genus *Nitophyllum* and its immediate allies, so far as the latter have been studied in this respect.

As has been said, very diverse forms of thallus occur among the *Rhodophyceæ*, and these forms give us no definite clue to the systematic position of any particular form, since there may be associated very diverse formations of thallus with one common plan of formation of fruits, and a similar formation of thallus with diverse fruit characters.

The *Rhodophyceæ* are sexually reproduced by male cells produced in *antheridia* which fertilise female cells called *carpogonia*. The antheridia are of very various forms, always giving rise superficially to the special male cells which contain each a single non-motile *pollinoid*. These male cells are formed in great numbers together, and they originate from the terminal cells of longer or shorter branches of the thallus-filaments (Fig. 62, *a*). The clusters of such

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branches, constituting the antheridia, are often collected into groups covering portions of the surface of the thallus. The surface may be depressed where they occur, and sometimes even flask-shaped cavities are formed, recalling the spermogonia of lichens (Fig. 84). The actual male cell itself is quite colourless but always nucleated. When ripe it opens at the apex and the contents issue forth as a round pollinoid, sometimes with a beak-like projection, and always with a nucleus. The occurrence of pollinoid cells in series, one above the other, in certain antheridia may be due to intercalary bipartitions, but possibly, on the other hand, to the successive abstriction of terminal cells which have remained attached in a chain. After the emission of the pollinoid, the supporting cell sometimes grows through and develops another male cell within the empty wall of the original male cell. No cilia have ever been detected on this membraneless pollinoid, though Schmitz and other observers have noted appearances that suggest the existence of some such organs. Guignard's recent observations, however, leave little doubt that the pollinoids are without cilia, and, moreover, that in some cases at least they are provided with a membrane at the time of their escape. So far as is known, however, they are wafted by the water much as the pollen grains of flowers are blown by the wind, and they do not usually become invested with a membrane until they reach the female organ.

The carpogonium itself is a single cell drawn out at one end into a long fine hair called the *trichogyne*, which projects from the surface of the thallus, and

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may be straight (Fig. 62, *b*) or have a spiral twist or two. The carpogonium is situated at the end of a row of usually three or four cells, the carpogonial branch, and the cells of this row immediately adjoining it acquire as a rule special characters. This carpogonial branch may be either superficial or within the body of the thallus. Fertilisation takes place by a pollinoid becoming attached to the apex of the projecting trichogyne (Fig. 62, *c*), and the cell-wall having been resorbed at the point of contact, the contents of pollinoid and trichogyne become united. The nucleus of the pollinoid disappears, and though its fusion with that of the carpogonium has not been observed, it may be inferred from analogous cases that it travels down the trichogyne to the carpogonial nucleus, and unites with it. The cell-wall then thickens at the base of the trichogyne and closes the communication; and the trichogyne slowly withers.

The farther development of the fertilised carpogonium is very various, but it is to be noted that, unlike the homologous bodies in other Algæ, it does not separate itself from its tissue connections, and its original cell-wall remains as its own proper membrane. Its farther development follows certain typical plans characteristic of the groups of *Rhodophyceæ*, and, while these are described in detail in the proper place, they may be briefly stated as follows. The carpogonium itself may in the simplest case give rise to a tuft of carpospore-bearing filaments; or there grow forth from it several simple or branched *ooblastema filaments* which conjugate with other cells, *auxiliary cells*, and as a result of this conjugation

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there are formed carpospore-bearing fruits; or the carpogonium conjugates with an auxiliary cell by means of a long or short (generally short) ooblastema filament, and the auxiliary cell then gives rise to the carpospore-bearing fruits. This remarkable and unique power of handing on the fertilising influence from the carpogonium which receives it to other (auxiliary) cells, which then behave like fertilised cells, is of great interest, since it appears to be without a parallel in nature. The filaments, *gonimoblasts*, which bear the carpospores always spring from fertilised cells, and the carpospore fruits may be either borne free or within special capsules, or immersed within the thallus, according to the group.

Non-sexual reproduction is effected by motionless spores called *tetraspores*, from their usual occurrence in fours within a sporangium. However, one only or two are formed in some cases; and the arrangement of the fours is a variable one. When all four spores are formed simultaneously they present together the form of a tetrad (Fig. 61, *a*); but when they are formed by successive bipartitions, two different types arise. If in the second division the walls are parallel to the first one formed, the result is a series of four spores, one above the other, called *zonate* tetraspores (Fig. 61, *c*). If the two secondary walls are not parallel, but perpendicular to the first formed, and not in one plane with each other, but at an angle of 90°, the result is the arrangement called *cruciate* tetraspores (Fig. 61, *b*). The tetraspores occur externally, and also within the cortical layers of the thallus. In some cases they occur in large numbers on definite

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branches called *stichidia*. This is the most common form of reproduction, and usually occurs in a succession of generations, while the plants bearing the sexual organs occur for the most part only at particular seasons.

The *Rhodophyceæ* are classified under four orders, viz., the *Nemalionaceæ*, the *Gigartinaceæ*, the *Rhodymeniaceæ*, and the *Cryptonemiaceæ*, according to the

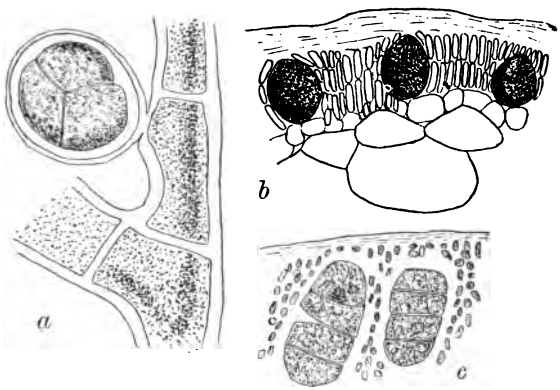


FIG. 61.—Tetraspores. *a*, tetrad (*Callithamnion*); *b*, cruciate (*Gracilaria*); *c*, zonate (*Catenella*). Highly magnified.

four main types of development of the carpogonium, and these orders are subdivided into families based on characters derived from the gonimoblasts and the whole cystocarp fruits. Since, as has been said, there is no constant correspondence of vegetative characters with reproductive characters, it is not possible to describe the former as distinctive of orders or families, but the prevailing kind of thallus will be indicated under each family.

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PLATE V.

1. PORPHYRA LACINIATA.

2. SCINAIA FURCELLATA.

3. NEMALION MULTIFIDUM.

4. NACCARIA WIGGHII.

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NEMALIONACEÆ.

General Characters.—The fertilised carpogonium gives rise directly to the gonimoblasts, which form erect or more or less spread out tufts of branches; these branches in one family (*Gelidieæ*) unite with neighbouring thallus cells or with specially developed auxiliary cells. The order is subdivided into four families, of which the three following are marine; one, viz. *Lemaneæ*, being exclusively freshwater.

Helminthocladieæ.

The gonimoblast is a short tuft of cell-filaments, either free or within a common gelatinous envelope (*Helminthora*); as a rule the terminal cells, and exceptionally also some of the cells next adjoining them, form the carpospores. After the terminal cell has emitted its carpospore, the supporting cell grows through it and produces within the old membrane a new spore-forming cell, and this process may proceed until the contents of the gonimoblast are exhausted. The gonimoblast is either external to the thallus or immersed within it, and does not possess a definite cystocarp wall, though sometimes a few enveloping filaments are wrapped about it. One genus, *Batrachospermum* is peculiar to fresh-waters, and *Chantransia* occurs in both marine and fresh-waters. Among the fresh-water species of *Chantransia* there have been described a considerable number of sporophytic shoots of *Batrachospermum* and protonema-like shoots of

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Lemanea, and these have been erroneously termed the "*Chantransia* forms" of these genera; but this means no more than if the protonema of a moss were to be

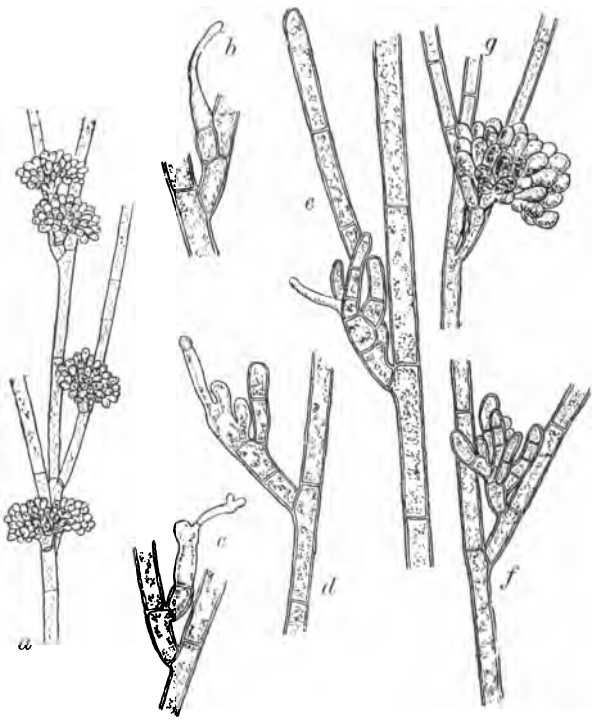


FIG. 62.—*Chantransia corymbifera*. *a*, filaments with antheridia; *b*, showing young trichogyne; *c*, the same fertilised; *d*, *e*, *f*, *g*, stages in development of cystocarp. Highly magnified. (After Bornet and Thuret.)

called its "*Conferva* form," or the prothallus of a fern its "Liverwort form." These growths of *Lemanea* and *Batrachospermum* have nothing to do with the

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valid generic type *Chantransia*. The species of *Chantransia* are mostly epiphytic and very minute, consisting of branching rows of cell-filaments springing from a membranous base and terminating upwards as a rule in fine long hairs. The reproductive processes have been fully studied in *Ch. corymbifera*. When the carpogonium has been fertilised it begins to sprout on one side and to produce the gonimoblast upwards. There is ultimately thus formed a naked corymbose fruit (cystocarp), the terminal cells producing the carpospores. The antheridia are in similar corymbose clusters. The so-called tetraspores remain undivided, are in fact monospores; but on germinating, as has been observed in *Ch. secundata*, the monospore first divides into four, and then very closely resembles a tetraspore. This division then proceeds in the same plane, thus giving rise to the membranous base of *Chantransia*, from which the erect filaments spring.

In *Nemalion* the fertilised carpogonium bulges upwards, and the upper portion is divided off as a new cell from the free surface of which the gonimoblast springs. In this genus and in *Helminthocladia*, a kind of envelope of filaments arises from the carpogonial branch and adjacent cells. In *Liagora* the thallus is slightly encrusted with carbonate of lime, but remains very slender and even viscid. It consists, as in *Nemalion* and *Helminthora*, of a number of united axial filaments, clothed with dense lateral branches at right angles to the axis. In all the genera, except *Chantransia*, the thallus is more or less gelatinous in consistence.

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The Geographical Distribution of the family is widespread, *Chantransia*, *Nemalion*, *Helminthora*, and *Helminthocladia* being represented in British seas, while *Liagora* is confined to tropical and warm regions of the sea, occurring however as far north as the Mediterranean.

Chætangieæ.

The gonimoblast is a convex, or concave, or spreading tuft of branched filaments, of which the terminal cells produce carpospores. The main difference between this family and the last is in the fact that the gonimoblast is immersed in the thallus and always enveloped in a special, thick, cellular fruit wall. The gonimoblast originates from one side only of the carpogonium as in *Chantransia;* at all events this is the case with *Scinaia*, in which it has been carefully observed.

Scinaia has a dichotomously branching thallus, consisting of a central axial tissue, from which there issue at right angles radiating, loose dichotomous filaments, constituting an intermediate tissue between the axial and peripheral tissues, the latter being composed of large colourless cells, with small ones filling up the spaces between them. Externally it is gelatinous. The cystocarps occur immediately beneath this peripheral tissue. *Chætangium* has a strong, vigorous, irregularly branched thallus with foliar expansions, often transformed into air-floats. *Galaxaura* and *Actinotrichia* have more or less encrusted peripheral tissues with slight annulate

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constrictions, or rugose markings. There are no foliar expansions, and the branching is dichotomous. *Galaxaura lapidescens* forms hard stony tufts of dense branches of almost as indurated a character as the Corallines.

The genus *Choreocolax* is one of the most remark-



FIG 63.—*a*, *Chætangium ornatum* slightly reduced; *b*, young carpogonial branch of *Scinaia furcellata* highly magnified. (*b*, after Schmitz.)

able among Algæ, since it contains at least one species (though it certainly shows a remarkable resemblance to *Harveyella*) that is wholly parasitic, viz., *Ch. albus* on *Rhodomela subfusca*. It has no chromatophores, and subsists entirely at the expense of its host-plant, so far as is known a unique

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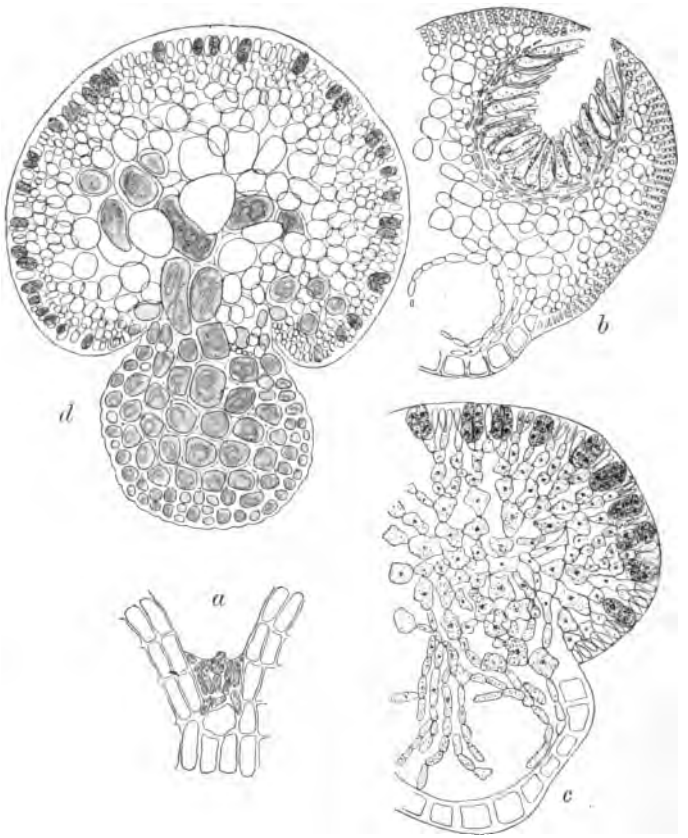


FIG. 64.—*a*, young plant of *Choreocolax Polysiphoniæ* (dark cells) penetrating host at angle formed by branches; *b*, cystocarp of same in section; *c*, tetraspores of the same (after Richards); *d*, *Choreocolax albus* with tetraspores; the dark cells, except the tetraspores, are those of the host. Highly magnified. (After Kuckuck.)

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occurrence among Algæ. Instead of killing the cells of the host affected, its parasitism appears to stimulate them to greater activity, as in the cases of hypertrophy caused by fungal parasites. *Ch. Polysiphoniæ*, if not a complete parasite is at least a partial one, and injuriously affects its host. These parasitic plants form exceedingly minute cushions of tissue externally while sending rhizoid filaments into the interior of the host, and on this outside cushion the tetraspores and cystocarps are borne. From his discovery and minute study of the latter in *Ch. Polysiphoniæ*, Richards has determined the position of this genus to be within *Chætangieæ* rather than *Gelidieæ*, as placed by Schmitz in his system. *Ch. Polysiphoniæ* grows in the axils of the branches of *Polysiphonia fastigiata*, and its rhizoid filaments penetrate and establish intimate connection, especially with the axial row of cells. The tetraspore-bearing plants exhibit certain differences in the peripheral thallus-cells from those of the cystocarpic plants (see Fig. 64, *b* and *c*).

The Geographical Distribution is confined to the temperate and tropical seas. *Scinaia* and *Choreocolax* are the only British genera, though they have otherwise a wide range. *Chætangium* occurs at the Cape of Good Hope, and *Galaxaura* and *Actinotrichia* are tropical and subtropical, the former being represented by one species in the Mediterranean.

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Gelidieæ.

The gonimoblast consists of much-extended, diffuse filaments which frequently unite with the thallus cells, these being in some cases specially developed as auxiliary cells. The terminal, carpospore-bearing cells occur in fertile sori or groups (like the hymenial layers of fungi), and bear the spores singly as a rule, rarely in short chains. The main difference between this type and the preceding families lies in the fact that this gonimoblast is not nourished exclusively by the fertilised carpogonium, but attaches itself in this growth to other cells, viz., cells of the thallus-tissue. A single gonimoblast is produced as a rule, but it ramifies abundantly, and lays under contribution either cells of the central axial row or the small-celled tissue that envelops it. From the ends of the branches of the gonimoblast the carpospores are produced, as described. During the branching of the gonimoblast a local enlargement of the thallus occurs, and within this the cystocarpic fruit is developed, with no special wall of its own, and bounded only by the sterile thallus-tissue. An opening is formed by the separation of the peripheral cells, through which the carpospores escape. In *Naccaria* the carpogonial branch exhibits a difference from the ordinary type. From the cells composing this branch short lateral branches arise, and the whole constitutes a definite system of cells. The carpogonium itself is relatively a small one, but before emitting the gonimoblast it unites with one of the

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neighbouring cells of its own branch, generally one larger than itself, and thus obtains more material for the first development of the gonimoblast.

The *Gelidieæ* embrace a considerable number of genera of very diverse stature and structure of thallus, ranging from the minute epiphyte (parasite ?) *Harveyella*, through slender and graceful forms like *Wrangelia*, to the stout-branched fronds of *Gelidium*, *Suhria*, and *Pterocladia*.

The Geographical Distribution is mainly in the north and south temperate zones, though the family is represented in all seas. *Harveyella*, *Atractophora*, *Naccaria*, *Gelidium*, and *Pterocladia* are British, and with a more or less wide range in northern seas; *Gelidium* however being of fairly general distribution, and *Pterocladia* typically represented in the Southern Ocean. *Caulacanthus* is a Mediterranean form, and *Porphyroglossum*, *Binderella*, *Wrangelia*, *Suhria*, *Acropeltis*, and *Ptilophora* are either confined to [illegible] (*Wrangelia*) find their [illegible] tropical (Java). [illegible] seas or at least (as [illegible] development in them.



FIG. 65.—*a*, carpogonium of *Naccaria hypnoides* (after Schmitz); *b*, *Gelidium corneum*.

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GIGARTINACEÆ.

General Characters.—The carpogonial branches and auxiliary cells occur in pairs, and the fertilised carpogonium conjugates by means of a short ooblastema filament with its auxiliary cell, which then gives rise to the gonimoblasts. The carpogonial branches and auxiliary cells rarely occur singly, but for the most part in groups of procarpia. The auxiliary cell therefore, not the fertilised carpogonium, is the central cell of the fruit, and the gonimoblasts, proceeding from it, branch copiously in the surrounding tissue of the thallus. The order is divided into three families, founded on characters derived from the gonimoblast and the cystocarpic fruit in general. The first of these, *Acrotyleæ*, consisting of the two exotic genera, *Acrotylus* and *Hennedya*, is distinguished by the development of a central cavity in the interwoven gonimoblast and sterile thallus-filaments, and this cavity is then lined with the terminal cells of the gonimoblast which here produce the carpospores. Both genera are further characterised by the possession of zonate tetraspores. The family *Gigartineæ*, which includes the following British genera, *Chondrus*, *Gigartina*, *Phyllophora*, *Stenogramme*, *Gymnogongrus*, *Ahnfeltia*, *Actinococcus*, *Callophyllis*, and *Callymenia*, most of them common on our shores, does not possess the cavity which characterises *Acrotyleæ*, but in its place there arises a dense, irregular, cellular complex of gonimoblast and sterile tissue, in the interior of which groups of

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PLATE VI.

1. PHYLLOPHORA RUBENS.
2. CATENELLA OPUNTIA.
3. CYSTOCLONIUM PURPURASCENS.
4. GIGARTINA MAMILLOSA.
5. CHONDRUS CRISPUS.

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much-branched fertile filaments form the carpospores, either from their terminal cells only or from the upper cells as well. The whole of this complex is generally enclosed within a definite cystocarpic wall.

Stenogramme, a small genus of wide distribution is represented on our shores by one somewhat rare

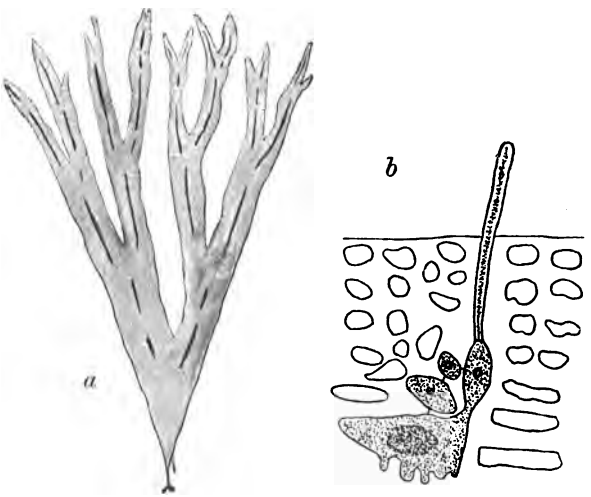


FIG. 66. — *Stenogramme interrupta*. *a*, plant reduced; *b*, carpogonium highly magnified. (*b*, after Johnson.)

species, *S. interrupta*. Its fruits occur in a more or less continuous midrib-like line on the frond. This line increases in distinctness and becomes convex as the fruits form. When the fertile line of procarpia is ready for fertilisation, the superficial layers of thallus-cells increase in numbers and ultimately form the fruit wall, while the cells in the centre of the frond increase in size and richness of contents.

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The latter cells nourish the growing cystocarp fruits, and when these are fully formed, the contents become very sparse.

In describing the development of the cystocarps

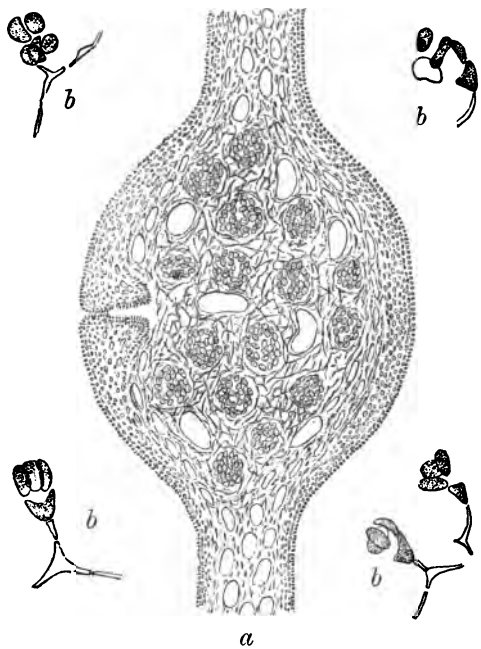


FIG. 67.—*Callophyllis obtusifolia*. *a*, cystocarp in section; *b*, carpospores. Highly magnified. (After J. B. Carruthers.)

of *Callophyllis*, Mr. John Carruthers says: "About the same time as the spore-clusters are beginning to develop, a further thickening of the cortex on both sides of the fruit commences. At one side of

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the fruit, at the place where the procarp originally was, the cells of the wall part asunder, and there arises a cylindrical canal through the whole thickness of the wall. The cells at the sides of this fruit-pore develop dense masses of hair-like cells at right angles to the pore, and nearly filling the whole of the canal. The pore is often formed very early, before the formation of the spore-glomerules, and before the spore-clusters have developed in size and have become fully matured spores. Such cell-clusters gradually develop into spores, the single cells become larger and more intensely coloured; and when they are mature, the connections between the individual spores are gradually loosened, the whole glomerule becomes disintegrated, and finally, the fully developed round spores are entirely free." Their escape through the pore is gradual, and in fact it often happens that some do not escape at all, and actually begin to germinate *in situ*.

In contrast with the well-developed, vigorous fronds of such genera as *Chondrus*, *Gigartina*, *Phyllophora*, *Stenogramme*, and *Gymnogongrus*, *Callophyllis* and *Callymenia*, the genus *Actinococcus* is of singular interest. *A. roseus* grows parasitically on *Phyllophora Brodiæi* forming externally small cushions which have been mistaken by some observers for the tetraspore fruits of the host plant. Its rhizoid tissue penetrates the inter-cellular spaces of the host, but its parasitism is obviously not so complete as that of *Choreocolax* (*Harveyella*?) *albus*. The antheridia and cystocarps are unknown, and the tetraspores only have so far been recorded. A

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closely allied genus *Colacolepis* is epiphytic on *Phyllophora nervosa* and *Ph. rubens.* It forms a small crust-like growth on the surface of its host, and is closely attached to its epidermal layer. It also is reproduced only by its tetraspores, so far as is known.

The family of *Rhodophyllideæ* is distinguished by



FIG. 68.—*Eucheuma spinosum* reduced.

the gonimoblast being divided into a number of *gonimolobes* which radiate from the auxiliary cell in all directions. These gonimolobes stretch out separately into the surrounding tissue of the thallus and their terminal cells, or in other cases the upper cells as well, form the carpospores. The auxiliary cell is frequently very large, and it forms the central cell of the whole fruit body.

There are only four British genera of this family,

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viz. *Cystoclonium*, *Catenella*, *Euthora*, and *Rhodophyllis*, but a considerable number of exotic types, such as *Solieria*, *Rhabdonia*, *Eucheuma*, *Erythroclonium*, and *Thysanocladia*, exhibiting among them the most diverse forms of thallus. In *Catenella* a large compound fruit is formed by many procarpia, each with

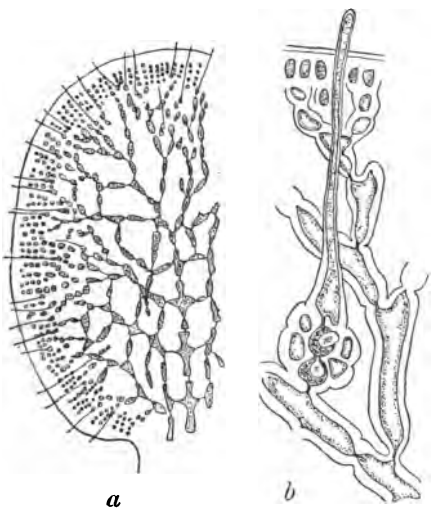


FIG. 69.—*Catenella opuntia*. *a*, section of fertile part of thallus showing numerous trichogynes; *b*, carpogonium with trichogyne highly magnified. (After Harvey Gibson).

its trichogyne, most of which are fertilised. The gonimoblast forms chains of carpospores which escape, since there is no ostiole, after rupture of the cortex "already weakened by the numerous apertures occurring in it through which the trichogynia pass to the exterior," as Prof. Harvey Gibson has described.

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The Geographical Distribution of the order is throughout all seas. The British genera have already been indicated, and the others, too numerous to particularise here as regards distribution, are some of them local, but most with a fairly wide range. The British forms have mostly a wide distribution elsewhere in the ocean.

RHODYMENIACEÆ.

General Characters.—More *Rhodophyceæ* probably conform to this type than to any other, and it is subdivided into a number of important families. The carpogonial branches and the parent cells of the auxiliary cells are developed in close proximity and form definite procarpia. After fertilisation has been effected the auxiliary cell is developed, and with it the fertilised carpogonium enters into conjugation by means of a very short ooblastema filament, the auxiliary cell sometimes sending forth a short process to meet it. Usually, and this is true of most *Rhodophyceæ*, the carpogonial branch is so curved that the carpogonium is brought into close vicinity with the auxiliary cell, and the ooblastema filament is therefore either very short or may be suppressed owing to the actual contact of these bodies. The auxiliary cell after this conjugation sends out the gonimoblasts towards the outside of the thallus, and the following families are established mainly on variations in this process, and its results in the form of cystocarpic fruits.

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PLATE VII.

1. Ceramium diaphanum.
2. Rhodymenia palmata.
3. Delesseria sanguinea.
4. Polysiphonia Brodiaei
5. Lomentaria articulata.

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Sphærococceæ.

Nearly all the members of this family have much branched fronds without foliar expansions, the branches being frequently robust and of dense texture. The gonimoblast is formed within the

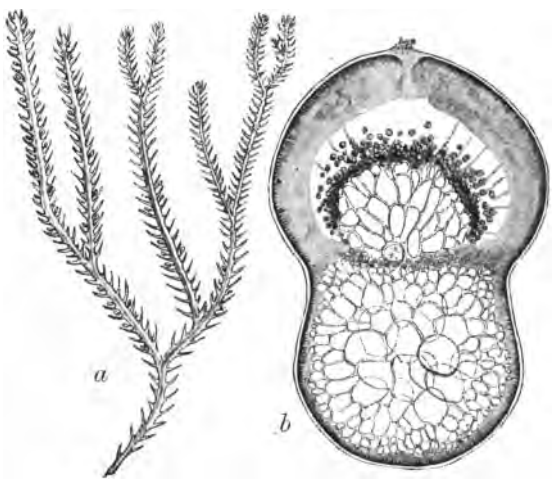


FIG. 70.—*a*, *Phacelocarpus Labillardierii* natural size; *b*, cystocarp of *Gracilaria confervoides* highly magnified. (After Thuret and Bornet.)

thallus, and produces its cystocarp within a wall formed of the peripheral thallus tissue which arches outwards and has an opening at the apex for the escape of the carpospores. The fruits consequently look like semiglobular swellings on the branches. Within this fruit-cavity and at its base there is formed a placenta from which the spores are produced, and its surface is free from the over-arching

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wall. The gonimoblast itself is a much branched tuft of closely packed filaments forming this convex placenta, and the carpospores are produced singly or in series on the points of the filaments at the free surface of the placenta within the cystocarp.

The Geographical Distribution is a very wide one and the forms are more abundant in the warmer seas, especially the two large genera *Gracilaria* and *Hypnea*. The other notable genera (*Sphærococcus*, *Corallopsis*, *Phacelocarpus*, and *Calliblepharis*) of the family have for the most part a similar distribution but are much more local. *Sphærococcus*, *Gracilaria*, and *Calliblepharis* are represented in British seas. *Gracilaria lichenoides* furnishes the substance called "Ceylon moss" from which at least one kind of Agar-Agar is prepared, a substance of much use in the cultivation of Bacteria.

Rhodymeniæ.

As in other families, so in this one, there is considerable diversity in the vegetative characters. *Rhodymenia*, of which *R. palmata* yields the edible "dulse" of our coasts, and *Plocamium* have fronds of conspicuous size, beauty, and firmness of texture, while such genera as *Chylocladia*, *Champia*, and *Lomentaria* with their hollow, tubular, and jointed fronds represent a simpler type. *Chylocladia* is well adapted to exhibit the typical constitution of the thallus of *Rhodophyceæ* built up of separate filaments, as Schmitz has established. By boiling a specimen in distilled water and afterwards pressing it under

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the cover-glass the points of the branches may be resolved into their component filaments, each with its apical cell and each exhibiting its history of division. All three genera (*Champia*, *Chylocladia*, and *Lomentaria*) have hollow tubular fronds filled with a gelatinous substance which also coats the

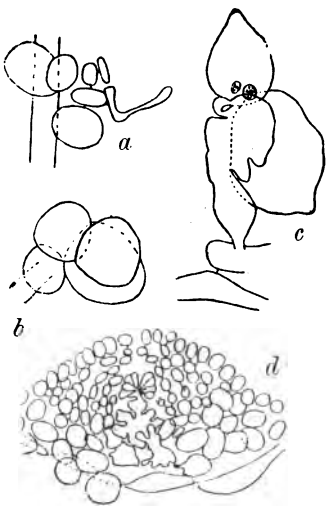


FIG. 71.—*a*, *Chylocladia kaliformis*, carpogonial branch with trichogyne ; *b*, fusion of cells of carpogonial branch to form one cell ; *c*, the fertilised auxiliary cell with the two nuclei near each other ; *d*, optical section of young fruit highly magnified. (After Hauptfleisch.)

outer wall. The first two have diaphragms interrupting the continuity of this tube, the last has none. With various minor modifications their reproductive processes, which have been studied in great detail by Hauptfleisch, are essentially the same and typical of the family. In *Chylocladia kaliformis* the

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carpogonial branch consists of four cells, and is formed, near the apex of a growing shoot, from one of the ordinary thallus cells. It curves backwards towards its point of origin and adjoins the basal cell from which the branch takes its rise. The trichogyne is also bent outwards, and penetrating the outer gelatinous coat of the thallus emerges into the open. Simultaneously with the formation of the carpogonial branch, the auxiliary cells are formed in the following manner. Two cells adjoining the one which bears the carpogonial branch each segment off externally one cell in such fashion that the carpogonial branch lies between them. The parent cells of these two auxiliary cells are usually large thallus cells, but in no way distinct from the ordinary thallus cells. Sometimes both, sometimes one only is connected by a pore with the cell which bears the carpogonial branch. Though both of the auxiliary cells are apparently equally adapted for its function, only one of them is utilised, and it happens exceptionally that only one is actually produced. In most cases the fertilised carpogonium is directed towards the auxiliary cell destined to be used, and the latter is then rich in contents. Immediately after fertilisation the carpogonium fuses first with the cell of its branch next it, and eventually with all four cells of the carpogonial branch, while at the same time all increase in size, as well as the cell which bears the branch. The great cell arising by this fusion is then farther increased by union with the cell that bears it, and only one large nucleus is discernible for

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the whole. While these changes are taking place the auxiliary cell also increases in size and richness of contents, while it approximates closely to the carpogonial cell. Sometimes, though not often, it



FIG. 72. – *Plocamium corallorhiza* natural size.

emits a conjugation-process towards the carpogonial cell, and when this is present the nucleus is to be seen within the process. More frequently the carpogonial cell emits a process (ooblastema filament) towards the auxiliary cell. Ultimately fusion takes

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place with the auxiliary cell and the nuclei of both unite.

The formation of the wall of the cystocarp begins when the carpogonium has been fertilised and the auxiliary cell is recognisable. Branched filaments arise from the thallus-cells in the immediate vicinity of the one which bears the carpogonial branch, and their apices meet over the auxiliary cell and the whole body assumes a globular form. It is noteworthy that these filaments have no pore connections with the carpogonial or the auxiliary cell. They develop into the cystocarp wall, which at first so confines and presses against the swelling carpogonial and auxiliary cell that the contents of the wall-cells next adjoining die off and their membranes swell up. At about this stage the auxiliary cell, after union with the carpogonial cell, fuses with its parent cell, and the whole united cylindrical body extends a kind of foot into the thallus beneath it. It may now for convenience sake be called the central cell. From its apical region there are now produced a number of marginal (gonimoblast) cells which have pore-connections with the central cell, and each of these gives rise to a carpospore. The central cell proceeds to unite below with cells of the thallus adjoining it, while it bears more gonimoblast cells on its upper and middle portions. In the ripe fruit only the outermost layer of cells of the wall remains, and these swell up and yield at the apex, permitting the egress of the carpospores.

Minor differences occur in the allied genera *Champia* and *Lomentaria*. Among these it may be noted

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that in *Lomentaria clavellosa* the fused carpogonial branch in uniting with the auxiliary cell first segments off a small cell which fuses with the auxiliary cell, but in *L. articulata* union takes place directly. Again, while in *Chylocladia* only single gonimoblast cells are given off by the central cell

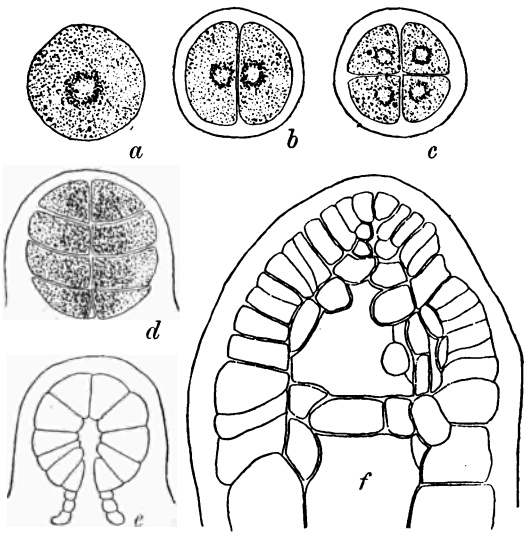


FIG. 73.—*Champia parvula*. *a*, *b*, *c*, *d*, successive stages in germination of carpospore; *e*, optical section of further stage in segmentation of spore; *f*, longitudinal section of apex of young plant highly magnified. (After Davis.)

for the formation of carpospores, in *Champia* and *Lomentaria* multicellular branched gonimoblast filaments are given off, and the terminal cells of these give rise to carpospores.

Mr. B. M. Davis has made a minute study of the development of the frond of *Champia parvula* from

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the carpospore, the early stages of which may be seen represented in Fig. 73.

The Geographical Distribution of the family is a wide one throughout both the north and south temperate zones and the tropical belt. Representatives penetrate also into the colder waters. *Rhodymenia, Cordylecladia, Lomentaria, Champia, Chylocladia* and *Plocamium* are all British and for the most part abundant on our shores.

Delesseriœ.

This family includes a number of the most beautiful red seaweeds, if indeed they are not the most beautiful of all Algæ. They possess leaf-like fronds, some of them with midribs (*Delesseria*) others with delicate lace-like or net-like expansions (*Claudea, Martensia, Vanvoorstia,* genera formerly reckoned among the *Rhodomeleœ*) and are all notable for their conspicuous and graceful forms. *Nitophyllum* and its immediate allies (see p. 202) differ from most other *Rhodophyceœ* in the occurrence of subsequent intercalary divisions of the thallus filaments. The procarpia are situated in the middle layer of the fronds, and the gonimoblast produces the carpospores within a fruit cavity formed of the thickened cortical layer of the thallus, perforated in the centre for the escape of the spores. The gonimoblast is somewhat indistinctly divided into several lobes, formed simultaneously or in succession, which bear the carpospores singly or in series terminally, or more rarely almost all the cells form spores.

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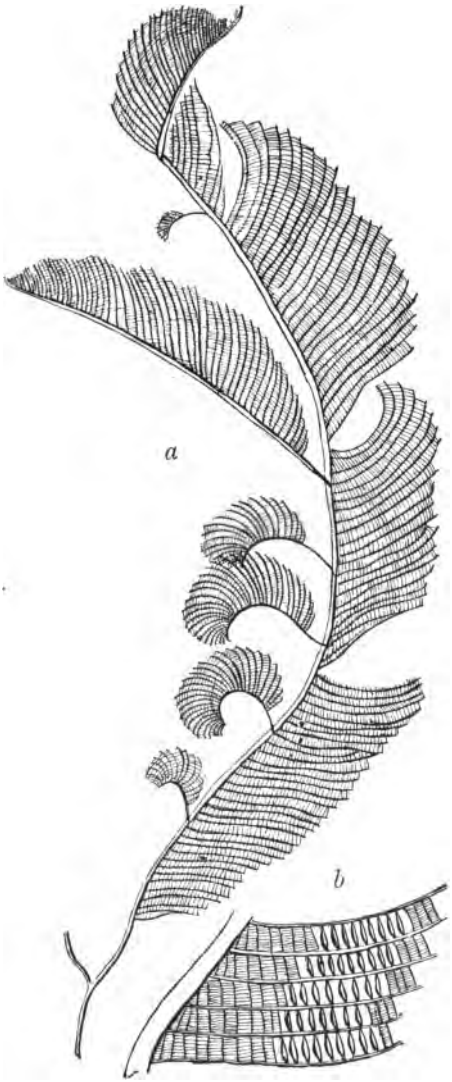


FIG. 74.—*Claudea elegans*. *a*, frond natural size; *b*, part of frond with cystocarps very slightly enlarged.

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The Geographical Distribution is well marked. *Nitophyllum*, *Delesseria*, and *Hydrolapathum*, the British genera, are widely represented, the two former in southern warm temperate seas as well as in the north. *Claudea elegans* occurs in Tasmania, and one small inconspicuous species, *C. multifida*, in Ceylon. *Martensia* occurs in South Africa, and *Grinnellia* is



FIG. 75.—*Martensia elegans* reduced.

confined to the Atlantic shores of North America. *Delesseria Amboinensis* is a singular freshwater form occurring in running streams at a considerable elevation above sea-level in Amboyna.

Bonnemaisoniæ.

This small family includes for the most part forms with long slender main shoots clothed with fine filamentous branches. The procarpia are situated in

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the cortical layers, and the fruit cavity is of similar character to that of the *Delesseriœ*. The gonimoblast is a copiously branching tuft of filaments of which the terminal cells bear large club-shaped carpospores.

Bonnemaisonia asparagoides is the only British form. *Asparagopsis Delilei* occurs in the warm North Atlantic; and of the other noteworthy genera *Ptilonia* and *Delisea* occur in southern seas.

Rhodomeleœ.

This is one of the most natural and best defined families of *Rhodophyceœ*, not only from its reproductive characters but to a considerable extent its vegetative structure as well. The thallus in most cases consists of tiers of cells in series, a central one with smaller pericentral cells of the same length grouped round it. Branching, commonly of a monopodial type, occurs, and the whole shoot is clothed more or less with fine hair-leaves if they may be so termed. Both antheridia and procarpia are formed on these hair-leaves, and are in the great majority of cases stalked. The cystocarps are therefore rarely sessile. In *Polysiphonia*, which may be taken as fairly typical of the rest of the family, the carpogonial branch is four or five-celled. The lowest of these cells becomes the auxiliary cell and the carpogonial branch so bends round that the carpogonium itself touches the auxiliary cell (Fig. 77). The other joint-cells adjoining the one which gave origin to the carpogonial branch

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divide and branch repeatedly, and so produce a body of cells enclosing the carpogonial branch. By division and growth of the cells that envelop this procarpium there is formed the wall of the more or less globular fruit, perforated at the apex



FIG. 76. — *Cliftonœa pectinata* natural size.



FIG. 77.—*a*, Diagram of procarp in *Rhodomeleæ* (*b* is the axial cell, *a* is the cell from which the carpogonial branch *e e e c* arises, and *d* is a branch cell which gives rise to sterile filaments); *b*, carpogonial branch of *Polysiphonia* (after Schmitz); *c*, *Dasya elegans* reduced.

and enclosing the gonimoblast. The gonimoblast is commonly a much suppressed tuft of cells on the upper, arched surface of which the carpospores are borne. These are generally ovate or club-shaped,

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very rarely two or three small, round spores in series, and they escape through the apical opening of the stalked fruit. The tetraspores are very frequently formed in stichidia. The family is a large one consisting of a considerable number of genera of conspicuous size and beauty of form, and some of the genera, such as *Polysiphonia*, *Laurencia*, and *Dasya*, are rich in species. *Pleurostichidium*, from New Zealand, is however an exception, being a minute epiphyte of quite different habit from the other genera, but of essentially similar structure.

The Geographical Distribution is world wide in the sea; some of the genera, such as *Polysiphonia*, have a range as wide as that of the family. The British genera, *Bostrychia*, *Rhodomela*, *Odonthalia*, *Laurencia*, *Halopithys*, *Chondria*, *Polysiphonia*, *Pterosiphonia*, and *Dasya*, are for the most part very common on our shores.

Ceramieæ.

This is one of the largest and most widely distributed families of Red Seaweeds, and members of it are everywhere common on coasts where Algal life is found at all. The thallus consists of single branched cell-filaments, sometimes with a cortex formed of rhizoid filaments (not a true cellular cortex). This false cortex is produced in the genera allied to *Callithamnion* by the outgrowth of rhizoid filaments from the basal cell of lateral branches, while in *Ceramium* and its immediate allies, such filaments spring from the upper ends (Fig. 78, *a*) of the cells of the thallus, forming a peripheral

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crown of cells covering the place where the parent cell is joined with the one above it. In some cases these filaments completely clothe the main cell row, in others they fail to meet and leave intervening parts bare. The procarpia are therefore external, and the gonimoblast is usually destitute of any envelope, but such does occur. The gonimoblast (of which there are usually two in each cystocarp) forms successively several lobes, of which nearly all the cells give rise to spores. *Callithamnion*, one of the commonest genera, may be taken as typical of the others in the matter of its reproduction. From one of the joint cells of the thallus there issue (besides the vegetative lateral shoot from its upper end) two small unicellular outgrowths from about the middle of the cell. From one of these a three or four-celled carpogonial branch proceeds (not from the thallus-cell itself, as usually stated). On the fertilisation of the carpogonium, the basal cells (or more rarely one of them) of the two original lateral outgrowths segment off each a daughter-cell, and these become the auxiliary cells. The fertilised carpogonium then extends a little sideways towards the auxiliary cells, and it also segments off its protruding parts as separate cells. These then conjugate with the auxiliary cells by means of an exceedingly

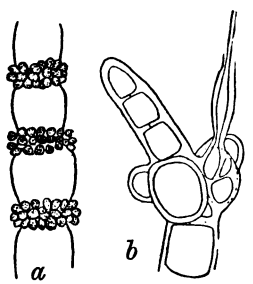


FIG. 78.—*a*, *Ceramium diaphanum* with nodal cells ; *b*, procarp of *Callithamnion gracillimum* highly magnified. (*b*, after Schmitz.)

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short ooblastema process. When the auxiliary cells have been thus fertilised they both divide, and the upper portions give rise to the two gonimoblasts of the cystocarp, while the lower portions fuse with the cells that bear them, and in some cases with the thallus-cell from which the fertile shoot originated.

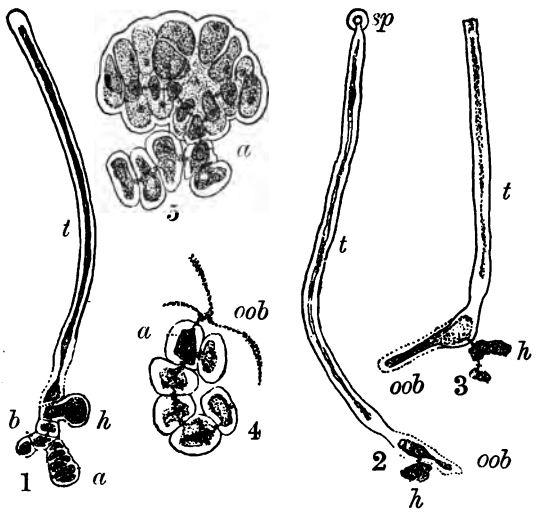


FIG. 79.—*Gloiosiphonia capillaris*, fertilisation and development of cystocarp; stages in order of numbers. *a*, auxiliary cell of procarpial branch; *b*, basal cell; *h*, hypogonous cell of carpogonial branch; *oob*, ooblastema—in (4) protoplast only; *sp*, pollinoid; *t*, trichogyne.

With some slight modifications this process is valid for the numerous genera and very numerous species of *Ceramieæ*. It includes such well-known genera, in addition to *Callithamnion*,* as *Lejolisia*, *Spermothamnion*,* *Sphondylothamnion*,* *Ptilothamnion*,* *Griffithsia*,* *Halurus*,* *Bornetia*,* *Monospora*,* *Pleonosporium*,* *Haloplegma*, *Ptilota*,* *Compsothamnion*,*

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*Plumaria,** *Ballia*, *Antithamnion,** *Crouania,** *Spyridia,** *Carpoblepharis*, *Ceramium,** *Microcladia,** *Rhodochorton,** and *Thamnocarpus*, those with an asterisk occurring in British seas. The family is of universal distribution in the sea, especially the genera *Callithamnion* and *Ceramium*.

CRYPTONEMIACEÆ.

General Characters. — As in the *Gelidieæ*, the fertilised carpogonium emits a relatively long ooblastema filament, which branches copiously in the thallus tissue. Its terminal cells or joint-cells conjugate each with single auxiliary cells, and from these the gonimoblasts spring. In *Gelidieæ* the filament which emerges from the carpogonium is itself the gonimoblast, and its conjugations with thallus cells appear to be of nutritive importance only, while in the *Cryptonemiaceæ* the fused cells give rise to the gonimoblast.

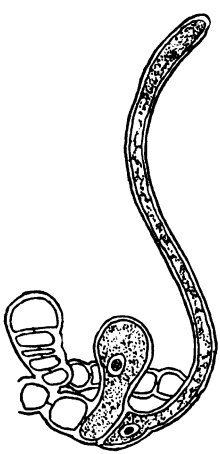


FIG. 80. — Young procarp of *Gloiosiphonia capillaris*. (After Schmitz.)

Gloiosiphonicæ, *Grateloupieæ*, *Dumontieæ*, and *Nemastomeæ*.

These four families, Figs. 79, 80, 81, are all characterised by the auxiliary cells being joint cells of secondary or primary filaments, and the carpogonial filaments usually of similar origin. The ooblastema filament

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PLATE VIII.

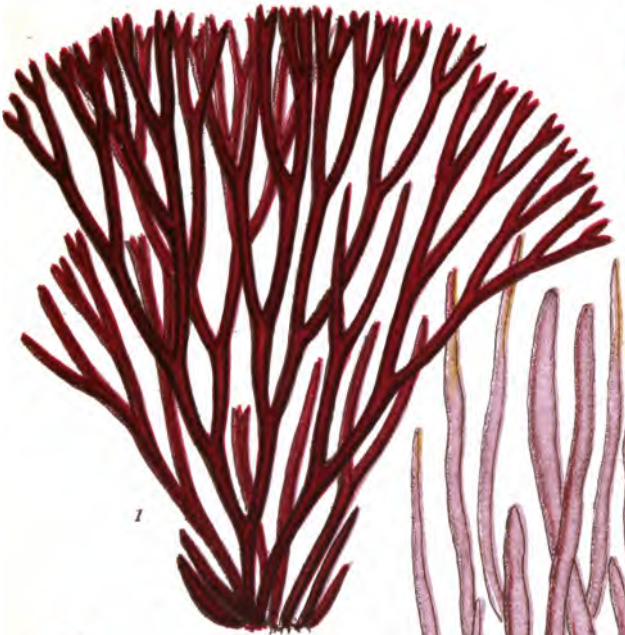
1. POLYIDES ROTUNDUS.

2. MELOBESIA MEMBRANACEA.

3. DUMONTIA FILIFORMIS.

4. CORALLINA OFFICINALIS.

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proceeding from the carpogonium successively fertilises a number of auxiliary cells, each produced on its own branch. After the conjugation of the ooblastema filaments and auxiliary cells, the gonimoblast that results is usually developed in the form of more or less definite gonimolobes, almost all the cells of which give rise to carpospores. The gonimoblast is in all cases within the thallus tissue. The geographical

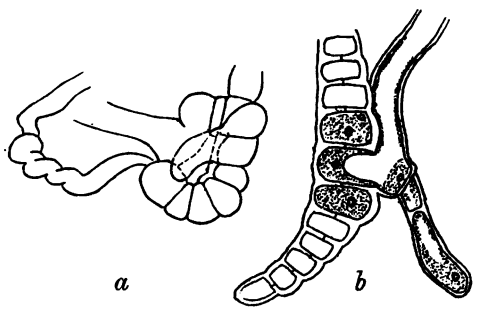


FIG. 81.—*a*, fertilised carpogonium of *Dudresnaya purpurifera*; *b*, ooblastema filament attached to auxiliary cell in passage (*D. coccinea*) highly magnified. (After Schmitz.)

distribution is fairly general, and the British genera are *Gloiosiphonia* (*Gloiosiphonieæ*); *Halymenia* and *Grateloupia* (*Grateloupieæ*); *Dumontia, Dudresnaya,* and *Dilsea* (*Dumontieæ*); and *Calosiphonia, Schizymenia,* and *Furcellaria* (*Nemastomeæ*).

Rhizophyllideæ.

This family, also a small one of fairly general distribution, is represented in British seas by only one genus, *Polyides.* The essential process of fertili-

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sation is the same in this genus as in *Dudresnaya* (Fig. 81). The carpogonial branches and the corresponding but more numerous branches that bear the auxiliary cells, are found together in special fertile portions of the cortex of the thallus. After fertilisation, this cortical tissue, having undergone

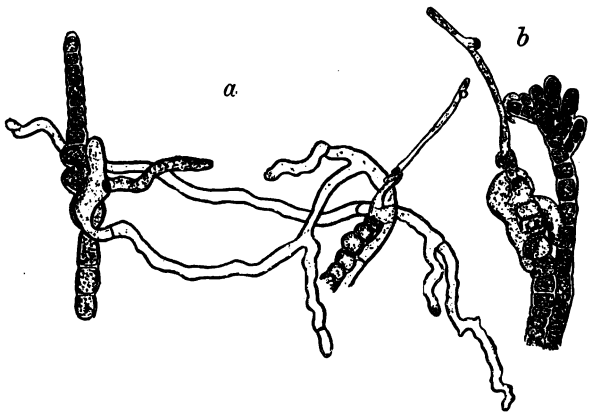


FIG. 82.—*Polyides rotundus*. *a*, procarp with trichogyne and ooblastema; *b*, ooblastema filament fertilising auxiliary cell highly magnified. (After Thuret and Bornet.)

considerable development, contains close together numerous gonimoblasts, nearly all the cells of which eventually give rise to carpospores.

Squamariecæ.

The thallus of the *Squamariecæ* is commonly minute and encrusting or consists of flat foliar expansions of tissue, in most cases encrusted with carbonate of lime. In this case, as in *Polyides*, the carpogonial branches

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and the auxiliary cells (joint cells of ordinary thallus filaments) are associated together in fertile regions of the cortex. The gonimoblasts are very minute and numerous, and produce carpospores in nearly all their cells. The family, though a small one, is of general distribution, and is represented in British seas by the genera *Petrocelis*, *Cruoria*, *Peyssonellia*, *Hæmatocelis*, and *Rhododermis*.

Corallineæ.

Of all *Rhodophyceæ* this family is the most easily recognised, from the strong incrustation of the thallus with carbonate of lime, producing a stony consistency. The different forms are, however, of the most various outward appearance. As in *Nitophyllum*, so here the thallus filaments undergo subsequent intercalary divisions. *Melobesia* is of encrusting habit, like some of the *Squamarieæ*, growing by marginal initial cells, at first circular, but afterwards becoming lobed and irregular through unequal development. *Lithophyllum* forms thin stony plates of erect habit, while *Lithothamnion* gives rise to massive stony branches (Fig. 83). Starting from a stone or shell, which the thallus subsequently encloses more or less as a kind of core, its branches frequently form massive structures, in some cases almost rivalling the animal corals in bulk. They occur in particular abundance with the true corals, and the species of *Lithothamnion*, *Melobesia*, &c., often act as a kind of mortar in holding together the reef-building corals. *Corallina*, *Amphiroa*, *Jania*, and *Cheilosporum*, are beautiful, stony,

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branched forms of a brittle character. The geological history of the family goes back to the Cretaceous

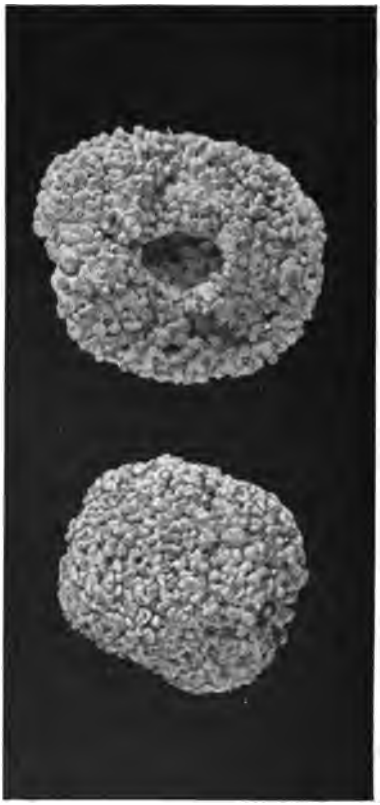


FIG. 83.—*Lithothamnion polymorphum* reduced.

times, and forms have been described, but with less certainty, from the early secondary rocks (Muschelkalk, Trias). They first appear, however, beyond

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doubt in the Senonian beds (near the top of the Cretaceous beds) as *Lithothamnion*, and are thus of the same proved antiquity as the Diatoms. It does not occur massively until the Tertiary rocks are reached,

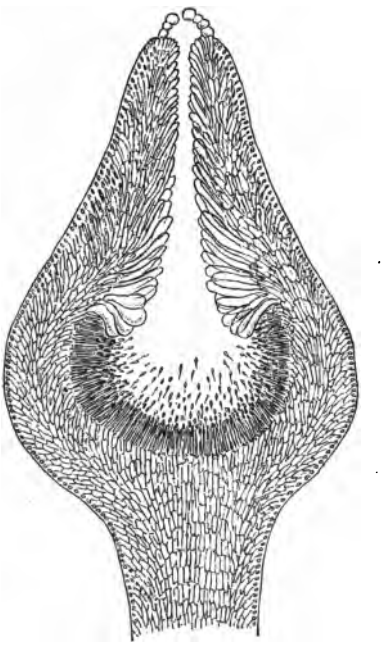


FIG. 84.—*Corallina mediterranea*, vertical section through antheridium highly magnified. (After Thuret and Bornet.)

when this contemporary genus occurs abundantly in the lower Eocene. The Leitha limestone (Miocene), the Pisolite limestone, and the nummulitic rocks, are largely composed of *Lithothamnion*.

Though of greater abundance in warm tropical

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seas, the Corallines have a much wider range than the animal corals, and occur in considerable numbers in the colder regions of the ocean. On British shores, *Corallina*, *Jania*, *Lithothamnion*, *Lithophyllum*, *Melobesia*, and a very minute form, *Schmitziella* (incrusting *Cladophora pellucida*), represent the family with a fair number of species.

The stony incrustation extends to all parts except the reproductive organs. Tetraspores, antheridia, and carpospores, are all formed in special conceptacular bodies (Figs. 84 and 85). In the flat encrusting forms these conceptacles appear as minute, wart-like outgrowths from the sterile part of the thallus; in *Corallina* they occupy the summits of the branches; and in *Amphiroa* they are lateral. In *Lithothamnion* these conceptacles are eventually overgrown by the increasing growth in thickness of the thallus, and in breaking down the stony substance they may be met with as small cavities representing the conceptacles of earlier periods of growth.

The carpogonial branches occur, together with numerous auxiliary cells, in special fertile portions of the cortex. The auxiliary cells are joint cells of peculiarly differentiated thallus filaments. On the fertilisation of the carpogonium all, or nearly all, the auxiliary cells near it become fused with it by means of the ooblastema filament, forming a large "conjugation cell." From its periphery minute gonimoblasts arise, bearing chains of carpospores. The cystocarp is here, therefore, a kind of syncarp, since it results from the combination of numerous auxiliary cells and their products into one common definite fruit,

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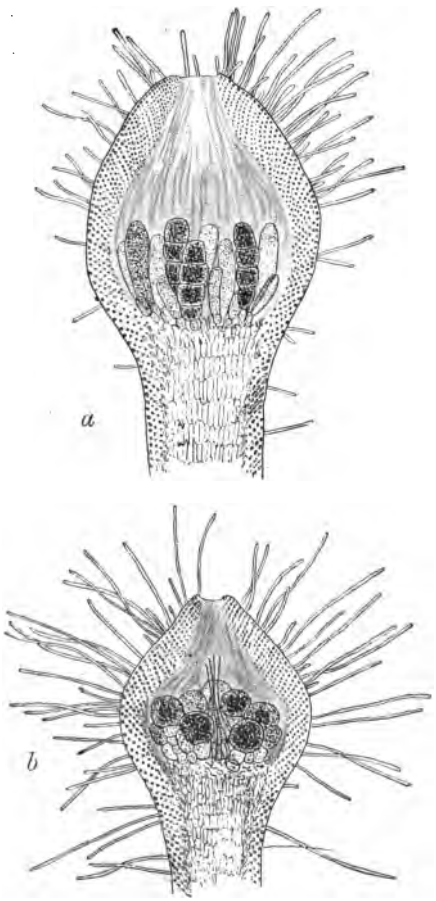


FIG. 85.—*Corallina mediterranea*. *a*, section of conceptacle with tetraspores; *b*, ditto of cystocarp highly magnified. (After Thuret and Bornet.)

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enclosed within a common cystocarp wall, with a single apical opening. As has been said, the antheridia and tetraspores are produced within similar conceptacles. The tetrasporangia arise at the base of the cavity, and either surround a central sterile bundle of filaments, or they occur in groups, separated by a wall of tissue from each other, and each with a separate apical pore (*Melobesia*).

BANGIACEÆ.

General Characters.—The thallus consists of cell-filaments (*Bangia*), or flat plates of one layer of cells and of irregular outline. Male reproductive bodies without cilia are produced within cells of the thallus, and they fertilise female cells specially distinguished from the thallus cells only by a short lateral protuberance. Non-sexual reproduction is effected by spores produced by the thallus cells, sometimes singly, sometimes after division of the parent cell.

There has been so much discussion as to the systematic position of the *Bangiaceæ*, and with so uncertain a result, that the terminology of the reproductive bodies is difficult of application. The claim put forward for their inclusion among the *Rhodophyceæ* does not appear to be fully established, while at the same time there is no little difficulty in assigning them a place among the *Chlorophyceæ*.

The Thallus.—The main argument for the inclusion of the *Bangiaceæ* among the *Rhodophyceæ* is derived

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from the colour of the chromatophores, which is in perfect agreement, but this is of purely physiological significance. On the other hand intercalary divisions occur in the cells of the thallus of *Bangiaceæ*, and though these occur also in *Nitophyllum*, *Corallineæ*, &c., the argument is not in favour of inclusion on this ground. The pits between the thallus cells of *Rhodophyceæ* are also absent from *Bangiaceæ*. Beyond colour therefore there is little support to be gained from the character of the thallus in favour of inclusion.

The Reproductive Organs.—The cells that become the female reproductive organs are indistinguishable from the ordinary thallus cells. The process of specialisation consists in a slight increase in size, but of no particular alteration in shape, except the acquisition of a very short lateral protuberance, called the homologue of a trichogyne by those who favour the inclusion of the order among the red seaweeds. The antheridia produce motionless unciliated pollinoids. In *Erythrotrichia* one of the thallus cells produces a small superficial cell, which is segmented off and becomes the mother-cell of a pollinoid. There is here a certain resemblance to the *Rhodophyceæ*, but in *Bangia* and *Porphyra* the pollinoids are produced by the repeated division (in all directions) of one of the thallus cells which has gradually lost its colour. Numerous small pollinoids are thus produced and set free by the dissolution of the membranes of the parent cells. The pollinoid fertilises the female cell on attaching itself to the short protuberance (trichogyne). An open communication is effected, and the contents of the

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pollinoid pass into and unite with those of the female cell. There is no development of gonimoblast, but the whole of this fertilised cell becomes a spore and emerges from its membrane, or it first divides once or twice and forms several spores. The whole of this process may represent a very much reduced or an ancestral Rhodophycean type, but there is a great gulf between it and the simplest form of indubitable Red Seaweed. The non-sexual spores, the so-called tetraspores, of *Bangiaceæ* leave us also in doubt. The whole of the contents of a single thallus cell go to the formation of one of the spores which are unciliated, at first without a membrane, but afterwards with one. In some cases there is a preliminary division (once or twice) of the thallus cell. It may be recalled that monospores (the undivided tetrasporangium) occur in certain *Rhodophyceæ*, but even then there is no conclusive evidence here for or against, though it leans towards inclusion. On the whole, and considering the difficulty of placing them elsewhere, the *Bangiaceæ* may be left beside the *Rhodophyceæ*, though not within the group.

The Geographical Distribution is world wide. It is however a small order with comparatively few species, though these are of very variable character. *Bangia*, *Goniotrichum*, *Erythrotrichia*, *Porphyra*, and *Diploderma*, are all British, and most of them abundant on our shores. The species of *Porphyra* furnish the edible Laver.

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SUB-CLASS V

CYANOPHYCEÆ

THE primitive forms of Algæ classified under this name possess in all cases a thallus of much simplicity, being unicellular, or composed of single rows of cells, nearly always embedded in definite gelatinous sheaths or gelatinous masses of indefinite outward form. The individual plants are in most cases associated together in colonies, the tendency to form gelatinous envelopes causing them to cohere in this fashion. Reproduction is typically a process of division of the thallus cells, though the precise mode of it, and of the liberation of the propagative bodies so formed, varies in the groups into which the *Cyanophyceæ* are divided. In *Chroococcaceæ* the cells are transformed into sporangia. A power of movement is exhibited, in the absence of cilia, by many members of the group, especially in the propagative cells, but this power is sometimes retained by the mature thallus, as in the case of *Oscillaria.* The colouring matter of the cells is a bluish-green substance, *phycocyanine,* in addition to chlorophyll.

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Other colours, such as purple, reddish purple, violet, yellow, and brown, are imparted to the plants by the coloration of their gelatinous envelopes. This colouring matter of the envelope has been called by Nægeli *scytonemine*, and is sometimes to be seen in the whole length of the sheath, sometimes only in part of it, but the peripheral part is more strongly tinged than the internal part, and it is displayed most vividly on the parts most exposed to light. The blue and red colours found in *Homocysteæ* and *Chroococcaceæ* are absent from the *Heterocysteæ*.

The colouring matter of the cells is not associated with definite chromatophores, as has been reported by several observers, the error having arisen from the presence of crystalloid bodies, or from the fact of the plant studied not being a member of the *Cyanophyceæ*. The protoplasmic contents of the cells are almost uniformly tinged with the colouring matter. This colour differs somewhat with the age of the plant and the degree of its exposure to light. It is ordinarily more greenish in young filaments with uncoloured envelopes, but with age it becomes more olive or even yellow. As has been pointed out by Bornet and Flahault, the other colours, seen in the protoplasm of herbarium specimens, are due to decomposition. No true nucleus has been observed, though its discovery has been reported by several observers. Zacharias and others have shown that the error is due to the presence in the centre of the cells of a colourless portion of protoplasm, which may be stained with hæmatoxylene. Its form, however, is not definitely limited

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like a true nucleus, and it has not been observed to display karyokinesis. Vacuoles do not appear ordinarily in the young cells, but with age, obscuration of light, or other unfavourable conditions, they arise and occupy a considerable part of the cell. It is not known, however, whether these vacuoles contain a cell-sap like those of other plants. Glycogen has been determined as present in the cells, but not starch.

If we consider the close relationship of the *Cyanophyceæ* to the Bacteria, it is not strange that theories of their polymorphism have arisen. It has been supposed for example that forms like those of *Chroococcaceæ* are often stages in the development of the higher *Cyanophyceæ*, and there are sufficient resemblances to give colour to such a view. But there is no more proof of it than this slight ground of speculation, except the equally slender support derived from the fact that the forms frequently grow in the same places. It requires actual observation of development to establish such a matter.

NOSTOCACEÆ.

This order is distinguished from the *Chroococcaceæ* by its multicellular thallus, and by the production of *hormogonia*, formed by the fragmentation of the filaments into mobile segments. The whole of a cell row is called a *trichome*, and the trichome with its envelope, which may be gelatinous, or even almost cartilaginous in consistence, is called the *filament*.

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It is most convenient to consider the *Nostocaceæ* under two families, viz. the *Heterocysteæ* and the *Homocysteæ*.

Heterocysteæ.

General Characters.—The cells of the trichome are differentiated into vegetative cells and into *heterocysts*, or cells incapable of farther development. The elongation of the trichome is by transverse division of all the cells (tribe *Nostoceæ*), or of a meristematic group of cells (tribe *Rivularieæ*). There is true branching only in the tribe of *Sirosiphonieæ*, effected by the division of cells parallel to the axis. Hormogonia, and spores endowed with the power of resting and of thus preserving the plant during unfavourable seasons and periods of dryness in particular, are the characteristic modes of reproduction.

The Thallus.—The vegetative cells of the trichome vary least in the tribe *Nostoceæ*, where they all appear to be very much alike; differences appear in those forms classified under *Scytonemeæ*, and are most marked of all in the tribe of *Rivularieæ*. The cells at the tip of a filament are generally shorter than at the base, where they attain an elongate cylindrical form. Cell-division takes place ordinarily when the cell attains its maximum length, but when growth is active the divisions succeed each other before that is reached and while the cells are still short. The envelope of the trichome (called the *sheath* in all the *Nostocaceæ*) may be mucilaginous, gelatinous, or cartilaginous in consistence, and there is considerable variety in its form and other characters, of service in

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classifying the genera and species, the thicker kind being frequently lamellated. The sheaths are at first colourless and transparent, and may remain so, but more often they become coloured as described. The

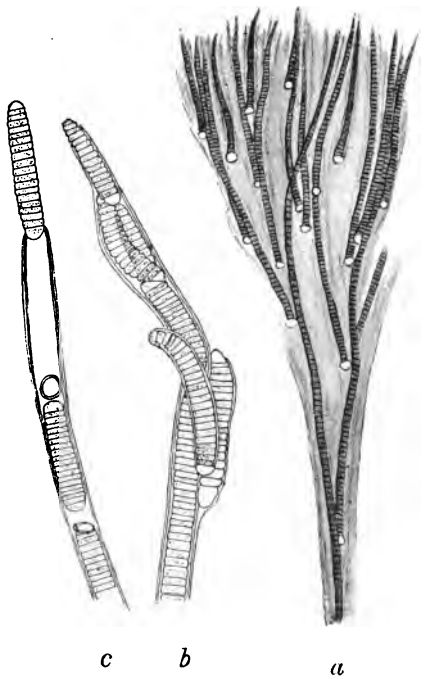


FIG. 86.—*a*, *Rivularia hospita*; *b* and *c*, hormogonia of *Calothrix pulvinata* highly magnified. (After Bornet and Thuret.)

heterocysts are special cells situated at the base of the trichome or intercalated in its course. They are bright green or light yellow in colour, have very little solid contents, and are commonly much larger than

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the ordinary vegetative cells, from which they may be farther distinguished by their greater refraction. They adhere to the sheath, and at the point of their attachment to the neighbouring cells there is a little button-like projection of cell-wall. Besides the true branching in the tribe of *Sirosiphoniæ* there are false branchings in other forms, occasioned by modes of growth, by the sticking of the heterocysts to the sheath, and by the development of hormogonia which have not escaped from the sheath, or have become fixed on the filaments. In the last case, of course, there is no sort of regularity.

Reproduction is most frequently—is ordinarily—effected by the production of hormogonia. These are mere segments of the trichome, to be distinguished from it with difficulty in some genera (*e.g. Nostoc. Anabaina*), but in others more specialised. In some cases the production of hormogonia terminates the existence of the thallus, and in fact involves its destruction; in others it begins at an early stage of development, while the filaments are still small, and proceeds more or less actively during the life of the plant. The hormogonia escape by sliding towards the opening at the end of the sheath. Some fix themselves on the parent plant, but most descend to the substratum. On coming to rest they either develop at once into a new filament, or rest for a longer or shorter time while their cells increase in size and their sheath grows in thickness, sometimes becoming larger than the ordinary filaments. In other cases the hormogonia divide and subdivide, while they elongate and multiply for a time before assuming

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the characteristic form of the filaments of the parent plant.

Spores are known in certain genera, and probably occur in all. They differ from the ordinary cells in their rounded form, greater size, and more granular contents, and their thick, coloured membrane. On germination the contents shrink from the wall and divide by parallel walls into a number of cells, and this short filament escapes by a perforation or circumscission from the parent membrane. It then becomes practically a hormogonium, and thus reproduces the plant. In a fresh-water form, *Sacconema*, the spore divides by perpendicular walls and gives rise to a globular colony like *Glœocapsa*, but Borzi, who records the observation, did not observe the development of this body into the normal form.

Homocysteæ or *Oscillarieæ*.

General Characters.—The characters which distinguish the *Homocysteæ* from the *Heterocysteæ* are mainly negative; they have no heterocysts and no spores. Their reproduction is solely by hormogonia.

The Thallus.—True branching, as in the *Sirosiphoneæ*, does not occur among the *Homocysteæ*, and since there are no heterocysts, there is no false branching of the type produced in the *Heterocysteæ* by the adhesion of the heterocyst to the sheath. Accordingly, in some of the genera the filaments remain simple, but false branching occurs frequently in the tribe *Vaginarieæ* and in *Plectonema* (*Lyngbyeæ*). The false branching in the former case arises when

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several trichomes, or bundles of trichomes, diverge at the extremity of their common sheath, in which they remain partially embedded, while the free parts become clothed each with a separate sheath. Where two trichomes thus emerge, it sometimes occurs that a fairly regular dichotomous false branching is produced. In the *Lyngbyeæ* false branching (in spite of the absence of heterocysts), arises from a breaking of the trichome, sometimes by its mere length, sometimes by a curvature of the filament, and the new ends breaking through the sheath grow out, or sometimes only one does this. The tribes *Vaginarieæ* and *Lyngbyeæ* have thus the first a terminal, the second a lateral branching.

The trichomes grow at all points, but generally towards the apex there are indications of apical growth in a greater number of short cells. At the apex itself the terminal cell, more or less conical or like a cupola in shape, has a thick protective outer membrane, and its presence or absence and its precise form afford a systematic character in classification.

The structure of the sheath has been very carefully studied in this group by M. Gomont, and his observations are probably generally applicable to all *Nostocaceæ*. The sheath and cell-wall proper exhibit different chemical reactions, and while the latter appears to resemble cutine, the sheath consists of a substance nearly allied to cellulose. At the same time the sheath appears to become cutinised, when it becomes coloured under the influence of light.

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Since the *Reproduction* by hormogonia has already been described under the *Heterocysteæ*, there is no distinctive character under this heading. The absence of spores has also been noted above.

The Geographical Distribution of *Nostocaceæ* is world-wide in fresh-waters and damp situations, on coasts and in mid-ocean. They are of rare occurrence in cold situations, and the littoral marine forms are generally to be found near high-water mark. The calcareous forms are more characteristic of fresh-waters than of the sea, and are especially abundant in hot springs. When they live in waters strongly charged with lime, the precipitation of carbonate of lime is caused by the absorption of carbonic acid. However, this precipitation occurs only where the Algæ do not find carbonic acid in sufficient quantity to meet the needs of vegetation. When it is abundant, as in certain mineral waters, the salt is precipitated only in very small quantities. The deposition may be round the individual filaments or so abundantly distributed as to envelop the whole thallus in a calcareous concretion. The genera *Mastigocoleus*, *Plectonema*, and *Phormidium*, contain species which perforate shells and other calcareous bodies in the sea. The pelagic *Oscillarieæ* occur in enormous abundance in the warm waters of tropical seas. From the periodical occurrence of *Trichodesmium erythræum* in great banks the Red Sea has obtained its name, and the same species and others allied to it have often been recorded from tropical seas in extraordinary floating masses. Most of the genera of *Nostocaceæ* which occur in the sea are known in British seas.

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CHROOCOCCACEÆ.

General Characters.—The *Chroococcaceæ* are distinguished from the *Nostocaceæ* not only by their unicellular character, but more particularly by the fact that they do not produce hormogonia, but unicellular reproductive cells. Typically cell-division does not occur in one direction only leading to the formation of trichomes, but the direction varies with more or less regularity, and since the daughter-cells remain together in colonies within the original envelope for a number of generations (*Glœocapsa*) irregular gelatinous masses are thus formed. The order is divided into two families, *Chroococceæ* and *Chamæsiphoneæ*, which may for convenience be treated separately.

The *Chroococceæ* are best known by the genus *Glœocapsa*. After each division of the mother-cell the daughter-cells may be free to develop independently, but usually they are held together by the common gelatinous envelope for a succession of generations. Spores are formed after the simultaneous change in habit of the whole colony of cells, and in place of the gelatinous membrane a thick membrane, rough on the outside, is developed. The spore repeatedly divides, and soon forms in this way a new normal colony of vegetative cells.

The *Chamæsiphoneæ* possess in *Hyella* a genus of perforating Algæ, which at first sight appears to be an approach to the *Nostocaceæ*, since the cells occur in filaments. They are, however, so many individual

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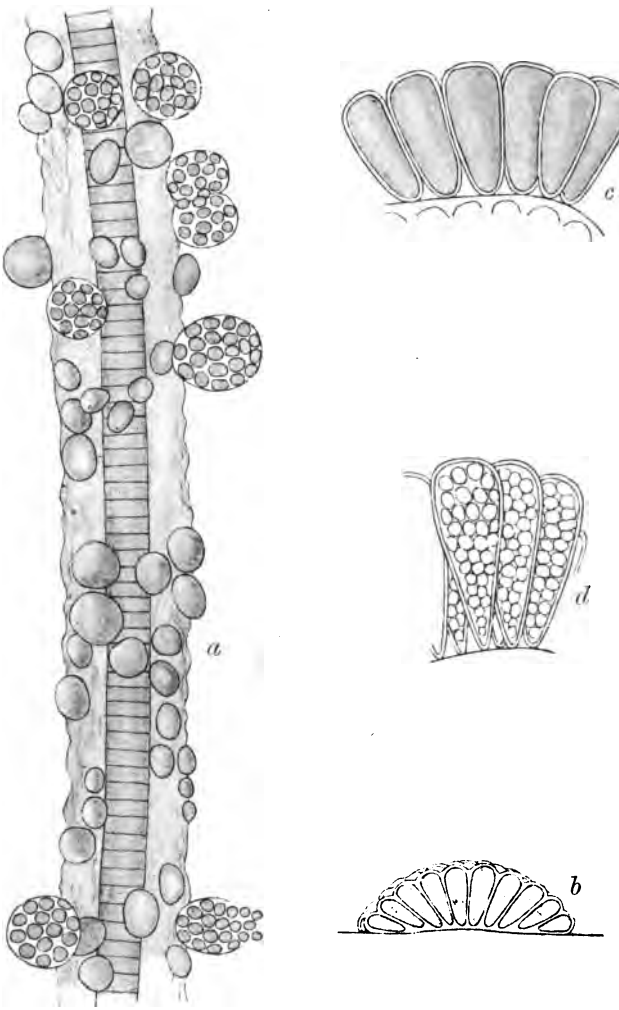


FIG 87.—*a, Dermocarpa Schousbœi* on *Lyngbya semiplena; b* and *c, D. prasina; d,* sporangia with spores highly magnified.

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plants, thus juxtaposed, each independent of the others, though inclosed within a common envelope, and not trichome-formations as in the *Nostocaceæ*. The filaments so formed by the colony ramify within shells often in company with *Gomontia* and *Mastigo-*

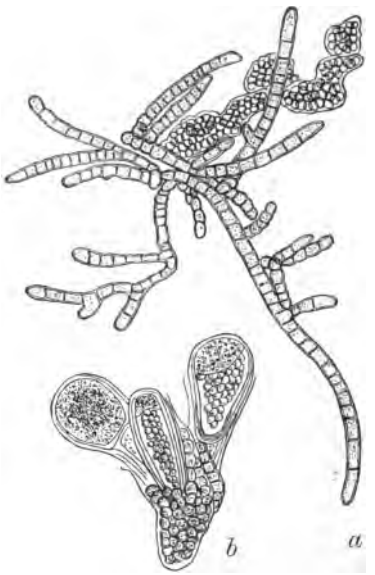


FIG. 88.—*Hyella cæspitosa*. *a*, young thallus, one of the branches divided into numerous cells; *b*, sporangia highly magnified. (After Bornet and Flahault.)

coleus, and effect the disintegration of the shell substance. Propagation is effected by the liberation of vegetative cells from the envelope (not in hormogonia), and by spores formed in sporangia by successive divisions of the protoplasm. *Dermocarpa* occurs as an epiphyte on other Algæ, and consists of clusters

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of roundish oval or pyriform cells grouped together. There is no vegetative propagation known, but the cells become sporangia in the fashion described for *Hyella.*

The Geographical Distribution of *Chroococcaceæ* is world-wide. *Glœocapsa, Polycystis, Hyella,* and *Dermocarpa,* occur in British seas. The two last genera are marine only ; *Hyella* known only in European waters, but *Dermocarpa* with a wider range.

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